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Terrestrial mollusks of Great Basin National Park, the Snake Range, Nevada, USA

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Abstract.—In this paper I report on the poorly known terrestrial mollusk fauna of Great Basin National Park (Snake Range) of the central Great Basin, USA. Mollusk species and numbers were recorded according to habitat affinities defined by a combination of rock type, geomorphology, plant communities, and water sources. A total of 6892 individuals representing 18 species of land snails and 1 species of slug were identified from 50 stations within GBNP during the period of spring 2014 through summer 2016. Mollusks were surveyed by 186 soil/litter samples and 1755 min of hand searching. Twelve habitat types included 2 xeric limestone/dolomite environments with conifer/aspen woodlands and no perennial waters (10 species in woodland litter and 15 species in rock slides below cliff faces). Two habitats dominated by granite/quartz rock with conifer/aspen woodlands and perennial streams supported 12 species in woodland litter and 13 species in rock slides. Eight species were recorded from a lower-elevation riparian habitat with cottonwood and shrubs. Two high-elevation habitats (approximately 3000 m) without perennial waters and dominated by bristlecone pine supported 1 species in limestone and 3 species in granite/quartz. A single high-elevation habitat (2800 m) of xeric pinyon pine/mountain mahogany and granitic/quartz rock supported 4 species. Two lower-elevation habitats (1800 m) supported 2 species in a sagebrush steppe, while no mollusks were found in pinyon pine/Utah juniper woodland. Two localized mesic habitats were associated with boggy streamsides and natural springs and supported 11 species each. The single species of slug *Deroceras laeve* and a species of succineid snail are restricted to these 2 habitat types. The 4 most common species of land snails (*Pupilla hebes, Vallonia cyclophorella, Euconulus fulvus,* and *Vitrina pellucida*) were present in 7 to 9 of the habitat types and represented 70% of the individual shells recovered. Taxonomic and biogeographical notes are included to allow for a better understanding of the species present in GBNP and the relationship of these species to the larger distribution of the terrestrial mollusks within Nevada and the Great Basin.

Resumen.—En este trabajo, informo sobre la fauna de moluscos terrestres poco conocida, del Parque Nacional de la Gran Cuenca (Great Basin National Park, “Snake Range”), en EU. Se registraron tanto las especies, como el número de moluscos de acuerdo con las afinidades al tipo de hábitat, definidos por una combinación de, (1) tipo de roca, (2) geomorfología, (3) comunidades de plantas y (4) fuentes de agua. En total se identificaron 6982 individuos, que representan 18 especies de caracoles terrestres y una especie de babosa, en cincuenta localidades dentro del Parque Nacional de la Gran Cuenca (GBNP, por sus siglas en inglés), durante la primavera del 2014, hasta el verano del 2016. Los moluscos fueron colectados en 186 muestras de suelo/hojarasca, después de 1755 minutos de búsqueda manual. Las muestras de suelo/hojarasca provinieron de doce tipos de hábitats incluyendo dos ambientes xerófilos de caliza/dolomita, y bosques de conífera/álamo, sin aguas perennes, que contuvieron 10 especies en hojarasca de bosque y 15 especies en rocas desprendidas bajo las paredes de acantilados. Dos hábitats dominados por piedra de granito/cuarzo, con bosques de conífera/álamo y corrientes perennes, albergaron 12 especies en hojarasca de bosque y 13 especies en rocas desprendidas. Se registraron ocho especies desde una elevación ribereña más baja, con álamos y arbustos. Dos hábitats de alta elevación (aprox. 3000 m), sin aguas perennes, dominados por pino longevo, contuvieron una especie en roca caliza y tres especies en granito/cuarzo. Un único hábitat de elevación alta (2800 m) de pino piñonero/cercocarpus xerófilos y roca granítica/de cuarzo, contuvieron cuatro especies de moluscos. Dos hábitats de elevación más baja (1800 m), alojaron dos especies en una estepa de artemisa. Mientras que no se encontraron moluscos en bosques de pino piñonero/*Juniperus osteosperma*. Dos localizados en hábitats mésicos asociados a laderas de arroyos pantanosos y manantiales naturales, albergaron once especies de moluscos cada uno. La única especie de babosa, *Deroceras laeve* y una especie de caracol Succineidae son endémica de estos dos tipos de hábitats. Las cuatro especies más comunes de caracoles terrestres (*Pupilla hebes, Vallonia cyclophorella, Euconulus fulvus* y *Vitrina pellucida*), estuvieron presentes en siete a nueve de todos los tipos de hábitats estudiados, y representan el 70% de las conchas individuales que fueron recuperadas. Las notas taxonómicas y biogeográficas son incluidas, para permitir un mejor entendimiento de las especies presentes en el GBNP, y de la relación de estas especies con la distribución más amplia de los moluscos terrestres presentes dentro del estado de Nevada y de la Gran Cuenca.

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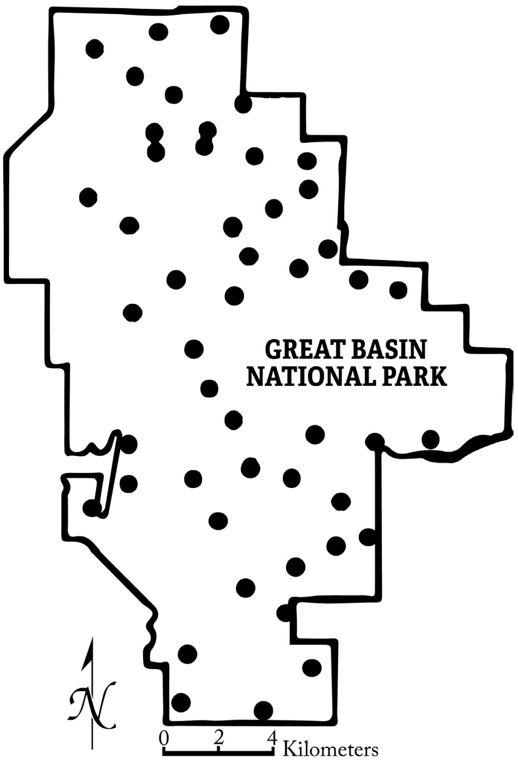

Fig. 1. Great Basin National Park, Snake Range, White Pine County, Nevada. Dots represent the 50 sample locations for mollusks in the park from spring 2014 to fall 2016.

The species richness and diversity of Nevada land snails and slugs are poorly known and incomplete (Pratt 1985, Ports 1996). The land snails found in the mountains of eastern Nevada and in Great Basin National Park (Fig. 1) represent a Rocky Mountain influence (Henderson 1931) much as do the species of subalpine conifers and montane mammals also found here today (Grayson 2011). Pratt (1985) reports on a preliminary survey of the land mollusks of the Snake Range including Great Basin National Park. Older records from eastern Nevada include the first record of *Oreohelix strigosa depressa* (Cockerell, 1911) from the state found on Baker Creek in what is today located in Great Basin National Park (Pilsbry 1939). From the Schell Creek Range just to the west of GBNP (Fig. 2), an endemic mountainsnail, *Oreohelix nevadensis* (S.S. Berry 1932), is recorded as the type locality as well as *Oreohelix hemphilli* (Newcomb, 1869) from the type locality of Hamilton in the White Pine Range (Fig. 2) (Pilsbry 1939). *Pupilla hebes* (Ancey, 1881) is a common species in the mountains of Nevada, with the type locality near Austin in central Nevada (Pilsbry 1939). This paper contributes information concerning the species richness and habitat affinities of terrestrial mollusks from eastern Nevada and increases the knowledge of the invertebrates found today in Great Basin National Park. Although not as diverse or abundant as many other groups of invertebrates found in GBNP today, terrestrial gastropods are often localized dispersers and dependent on specific microhabitat conditions (Nekola 2003), making them important indicators of the impacts of drought (Chang and Emberton 1993) and wildfires (Beetle 1997). Terrestrial gastropods in the western United States are important consumers of live and dead plant material, rotting wood, scat, fungi, and algae. They are also a source of prey for birds, small mammals, and insects. Since land snails use calcium carbonate to build their shells, they act in the ecosystem calcium cycle. They are useful indicators of ecosystem health and land use, and some species act as an intermediate host for some mammalian parasites (Jordan and Black 2012).

METHODS

Study Area

Great Basin National Park (GBNP) was established by Congress in 1986 under the management of the U.S. National Park Service, Department of Interior. GBNP encompasses the southern Snake Range (Lehman Creek Visitors Center: 39°00′22.2″N, 114°13′07.8″W, 2080 m) (Google Earth 2016) located in east central White Pine County, Nevada (Fig. 2). Encompassing 310 km^2, the GBNP (Great Basin National Park 2017) includes the second highest peak in Nevada, Wheeler Peak at 3982 m, with several other high-elevation peaks dominated by granite and quartzite rock. Limestone and dolomite geomorphology occur in the southern end of the park, in canyons on the west side, and on cliff faces in lower Baker Creek. As with many of the Great Basin mountain ranges, the Snake Range is a metamorphic core complex with Spring Valley on the west side at approximately 1800 m elevation and Snake Valley on the east at approximately 1600 m (Harris et al. 2004). Eight major drainages occur predominantly on the eastern side of the park, while the lower boundary of the park averages 1800 m elevation on the east slope and 2500 m elevation on the steeper west slope (Fig. 1). The park was established to preserve representative ecosystems of the Great Basin Desert, educate the public concerning the natural flora and fauna, and preserve cave systems and archeological history (Baker 2012).

Survey Localities and Sampling Procedures

Fifty localities were surveyed in GBNP during 28 field trip days conducted during the months of May through September 2014–2016 (Fig. 1). Litter samples were collected in a nonrandom fashion to maximize species richness and abundance. Only microhabitats where land snails were likely to be found were sampled (Nekola 1999, Cameron and Pokryszko 2005). A 1-m^2 grid was used to collect 186 soil/litter samples into 3.8-L plastic ziplock bags. Species richness and percent abundance was recorded by collecting shells within each 1-m^2 grid. Approximately 4–12 cm of soil and litter was collected from within the grid from each of the 4 corners and the center, using a hand rake.

Soil/litter samples were air dried and passed through a sequence of 5 graded nested sieves with square spaces of 0.2, 0.5, 0.8, 1.6, and 3.2 mm^2. Only the number of live animals and whole shells of each species were counted from each sample. Shell fragments were not included in determining the number of land snails per sample. A total of 186 soil/litter samples (bags) were hand searched for specimens. A total of 6829 shells and 7 slugs were collected during the survey. Specimens were sorted and separated into individual vials, then labeled by species and locality. Specimens were identified using a 40× dissecting scope and keys from Pilsbry (1939, 1946, 1948) and Burke (2013), while following the taxonomy as found in Turgeon et al. (1998). Representative specimens are deposited into the GBNP natural history collection. Voucher specimens of the 19 species of mollusk are catalogued with the Santa Barbara Museum of Natural History, California, under the following numbers: SBMNH 461177, 461188, 461193, 461196, 462870, 462875, 462888, 462892, 462918, 462937, 462953, 465271, 467212, 467229, 468895, 468904, 468927, 468953, and 613928.

A total of 1755 min of visual/hand searching was also conducted during the survey for large land snails and slugs, which are typically not recorded by sifting soil/litter samples (Cameron and Pokryszko 2005). In this study visual/hand searching was most effective with the larger mountainsnails (*Oreohelix)*, the 7 individuals of the slug *Deroceras laeve* (Muller, 1774), and live snails attached to moist vegetation associated with spring and boggy streamside habitat.

Twelve habitat types were determined from GBNP based on rock types (limestone/dolomite and granitic/quartz), geomorphology (rock slides below cliff faces and dry and perennial drainages), water sources (springs, boggy streamsides, ephemeral and perennial streams), and plant communities (Table 1).

RESULTS

Faunal Descriptions and Biogeographical Patterns

Leaf litter/soil sampling by grid and visual searches yielded 6894 individuals representing 18 species of land snails (including a species from the family Succineidae) from 186 soil/litter samples representing 50 localities throughout the park. Eighteen species of land snails and 1 species of slug representing 12 families of mollusks were documented (Table 1).

FAMILY SUCCINEIDAE.—These taxa were found in small numbers from 3 of the 12 habitat types (Table 1). The ambersnails in North America display a great deal of shell variation, making it difficult to accurately identify them at the genus and species levels (Burke 2013). Identification by genitalia characters represents one way to delineate individuals at the species level (Pilsbry 1939). Specimens collected at GBNP were not dissected due to their small size; however, the shells examined are small, globuse, 5–6.5 mm long, and have 3–3.5 whorls and a broadly ovate aperture (Burke 2013). While these features would suggest the genus *Catinella,* there are few recent records from eastern Nevada of this family, and those are based on shell characters (Pratt 1985).

PUPILLA HEBES (ANCEY, 1881).—The Rocky Mountain Column is the most abundant land snail in the park, with 1897 shells collected from 9 of the 12 habitat types surveyed,

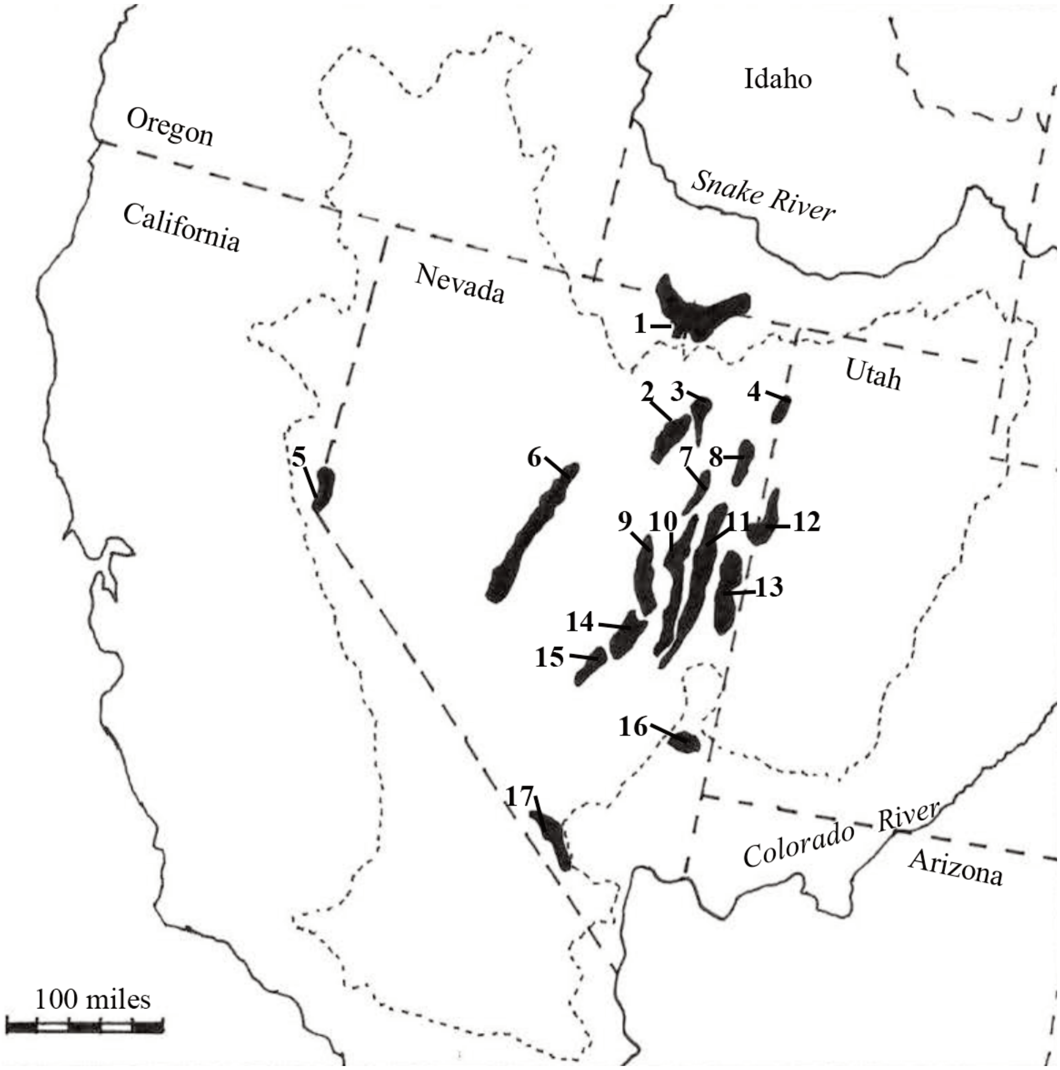

Fig. 2. Locations of mountains in the Great Basin as mentioned in the text. 1. Jarbidge Mountains. 2. Ruby Mountains. 3. East Humboldt Range. 4. Pilot Range. 5. Carson Range. 6. Toiyabe Range. 7. Cherry Creek Range. 8. Goshute Mountains. 9. White Pine Range. 10. Egan Range. 11. Schell Creek Range. 12. Deep Creek Range. 13. Snake Range (location of GBNP). 14. Grant Range. 15. Quinn Canyon Range. 16. Clover Mountains. 17. Spring Mountains. The dotted line represents the boundary of the Great Basin. With permission by Univ. of California Press and modified from Grayson 2011.

making up 27% of the total shells collected (Table 1). The type locality for this species is near Austin in central Nevada (Pilsbry 1948), and the species is widespread throughout the mountains of the state (Ports unpublished data; Ports 1996). Nekola et al. (2015) used both DNA sequencing and conchology to show that *Pupilla hebes* and *Pupilla blandi* (E.S. Morse, 1865) cannot be separated solely by aperture lamellae and that *P. blandi* is found east of the Rocky Mountains while *P. hebes* is found in the Great Basin. Pratt (1985) and Ports (1996) recorded *P. blandi* in Nevada; however, this record has since been proven incorrect (Nekola personal communication). The specimens of *Pupilla* collected in GBNP are identified as *P. hebes* based on shell microsculpture (sharp parallel ribs on the peripheral whorl) as shown in Nekola et al. (2015). A single population of *P. hebes* at GBNP contained shells varying from no aperture lamellae to shells with 1 to 3 lamellae, which supports the

TABLE 1. Mollusk species examined at Great Basin National Park, Nevada, during the period of May 2014 to September 2016, and the number of shells/individual slugs recorded from 12 habitat types: I. Limestone/shale, ephemeral drainage, conifers, aspen, shrubs, and grasses. II. Limestone/shale, rock slides, cliff bases, conifers, shrubs, and grasses. III. Granite/quartz, perennial stream, conifers, aspen, shrubs, and grasses. IV. Granite/quartz, rock slides, conifers, aspen scrub, shrubs, and grasses. V. Granite/quartz, perennial stream, cottonwood, shrubs, and grasses. VI. Limestone/shale, dry woodland, bristlecone pine, shrubs, and grasses. VII. Granite/quartz, dry woodland, bristlecone pine, and grasses. VIII. Granite/quartz, mountain mahogany, pinyon pine, shrubs, and grasses. IX. Springs in aspen, willow, shrubs, forbs, and grasses. X. Boggy streamsides, willow, shrubs, forbs, and grasses. XI. Sagebrush, rabbitbrush, bitterbrush, forbs, and grasses. XII. Pinyon pine, Utah juniper, dry bare ground, sagebrush, grasses.

Mollusk species	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Succineidae, Amber snails					3				2	7		
Pupilla hebes	346	606	480	206	197			14	6	24	18	
Gastrocopta pilsbryana	6	10										
Vertigo modesta concinnula	8	48	87	104					41	12		
Vallonia cyclophorella	415	442	105	103	43	41		12			60	
Vallonia gracilicosta	2	10										
Microphysula ingersolli		5	30	6			1					
Oreohelix strigosa depressa		328	310	26						15		
Oreohelix hemphilli	205	275		8								
Oreohelix nevadensis		22										
Paralaoma servilis			14	26	21				6			
Punctum minutissimum		85	10	15				8		4		
Discus whitneyi		25	62	26	2		1		8	10		
Euconulus fulvus	774	106	42	20	6				11	19		
Zonitoides arboreus	12	9	7	10	2		1		4	5		
Hawaiia minuscula	42	42		3								
Vitrina pellucida	68	338	102	93	84			14	13	42		
Derocerus laeve									5	2		
Total shells/live mollusks	1878	2351	1249	646	358	41	3	48	98	142	78	0
Species richness	10	15	12	13	8	1	3	4	11	11	2	0
% total shells/habitat	27	34	18	9	5	1	0.1	1	2	2	1	0
Number of soil/litter samples	33	42	30	25	14	6	4	5	***	11	8	8

***Refers to hand-picked shells and slugs with no soil/litter samples.

variability in this character as suggested by Nekola et al. (2015).

GASTROCOPTA PILSBRYANA (STERKI, 1890).—The Montane Snaggletooth typically occurred at higher elevations in GBNP in plant communities associated with limestone/dolomite rock types in small numbers (Table 1). The presence of this species in the GBNP represents the first record for Nevada. The genus *Gastrocopta* has not been recorded from the Ruby Mountains (Ports 1996) but has been recorded from the Quinn Canyon Range and the Spring Mountains to the south (Fig. 2) (Ports unpublished data).

VERTIGO MODESTA CONCINNULA (COCKERELL, 1897).—The Mitered Vertigo was recorded from 8 of the 12 habitat types (Table 1). The Mitered Vertigo individuals found in the park have an aperture dentition of 2-1-2 with 2 elongate palatals and a flared peristome, while some shells have an aperture dentition of 1-1-2 (Pilsbry 1948). Using DNA analysis rather than shell characters, Nekola et al. (2018) places the species *V. concinnula* into the subspecies *Vertigo modesta concinnula* and describes the ecology as mesic to dry upland woodlands. Based on this analysis, there is only one species of *Vertigo* in GBNP found in both high-elevation mesic woodlands and in wet springs (Table 1). *Vertigo modesta concinnula* and *Vertigo ovata* (Say, 1822) are recorded from the Ruby Mountains of northeastern Nevada (Ports 1996), and *Vertigo modesta castanea* is recorded from the Jarbidge Mountains of northern Nevada (Fig. 2) (Ports unpublished data). Otherwise, few records exist for the *Vertigo* species in Nevada.

VALLONIA SPP.—*Vallonia cyclophorella* (Sterki, 1892), the Silky Vallonia, was recorded from 8 of the 12 habitat types, making it the second most abundant land snail in the park, with 17% of the total shells (Table 1). In the GBNP, these whitish shells range in diameter from 2.5 to 3.2 mm and are ribbed with a thin reflective peristome; the last whorl descends from the penultimate whorl. The Silky Vallonia has been recorded from the Ruby Mountains (Ports 1996) and several mountains throughout western, central, and southern Nevada (Pratt 1985) and on the east slope of the Sierra Nevada (Carson Range; Fig. 2) (Ports unpublished data). A second species, *Vallonia gracilicosta* (Reinhardt, 1883), the Multirib Vallonia, was collected from 2 of the 12 habitat types but in much smaller numbers, making up <1% of the total shells (Table 1). This species was distinct in having a thickened peristome, distinct cuticular riblets, and an aperture that descends only slightly below the penultimate whorl. While not recorded for the Snake Range or the Ruby Mountains (Pratt 1985, Ports 1996), this species has been found in the Jarbidge Mountains (Nekola personal communication) as well as in Montana (Hendricks 2012) and the Rocky Mountains (Pilsbry 1948).

MICROPHYSULA INGERSOLLI (BLAND, 1875).—The Spruce Snail was recorded in small numbers from 4 of the 12 habitat types, comprising <1% of the total shells (Table 1). This species is uncommon in the Ruby Mountains of northeastern Nevada (Ports 1996), north to the Jarbidge Mountains along the Nevada/Idaho border (Ports unpublished data), the Schell Creek Range just to the east of GBNP (Pratt 1985, Ports unpublished data), and south to the Clover Mountains south of GBNP (Fig. 2) (Pratt 1985). It has not been found in central, western, or far southern mountains of Nevada (Ports unpublished data).

OREOHELIX STRIGOSA DEPRESSA (COCKERELL, 1890).—The Great Basin Mountainsnail was found in 4 of the 12 habitat types, making up 10% of the total shells collected. This is the typical subspecies found in the Wasatch Mountains of Utah (Chamberlin and Jones 1929), west to the Deep Creek Range, the Pilot Range (Fig. 2) (Ports unpublished data) along the Nevada-Utah border, the Ruby Mountains (Ports 1996, 2004), south to the Snake Range (collected "near Lehman Cave" which is inside GBNP today) (Pilsbry 1939), and southwest to the southern Egan Range (Ports unpublished data). This subspecies was not found in northern (north of the Humboldt River), central, southern, or western Nevada mountains (Fig. 2) (Ports unpublished data).

OREOHELIX HEMPHILLI (NEWCOMB, 1869).—The Whitepine Mountainsnail was found in 3 of the 12 habitat types, making up 7% of the total shells collected. The center of its range appears to be in eastern Nevada (Ports 2004), extending into central Nevada in the Toiyabe Mountains (Ports unpublished data), north to the Ruby Mountains (Ports 1996), and southeast to the Clover Range (Fig. 2) (Pratt 1985). This species does not appear to be present north of the Humboldt River in northern

Nevada, nor in western Nevada (Carson Range, Fig. 2) (Ports unpublished data). The type locality for this species is in the White Pine Range (Fig. 2) to the west of GBNP (Pilsbry 1939).

OREOHELIX NEVADENSIS (S.S. BERRY, 1932).—The Schell Creek Mountainsnail was found at only one locality in the park and apparently consists of a single colony making up <1% of the total shells collected. This species is endemic to eastern Nevada and the type locality is west of GBNP in the Schell Creek Range (Fig. 2) (Pilsbry 1939). The shell is large for this genus as it occurs in Nevada—12 to 18 mm in diameter, with a low-to-depressed spire, an angular-to-round body whorl, and a series of spiral "beaded welts" on both the base and apical body whorl surfaces (Pilsbry 1939). These shell characters are also seen in *Oreohelix loisae* in the Goshute Mountains (Ports 2004), as well as in some *Oreohelix* populations in the Cherry Creek Range to the northwest of the park (Fig. 2) (Ports unpublished data). Pilsbry (1939) suggests that the Schell Creek Mountainsnail is similar in shell anatomy to *O. haydeni hybrida*, which is found in the northern portion of the Wasatch Mountains (275 km west, Fig. 2).

PARALAOMA SERVILIS (SHUTTLEWORTH, 1852).—The Pinhead Spot was found in 4 of the 12 habitat types in low numbers, making up approximately 1% of the total shells (Table 1). This species was reported under the synonym *Punctum conspectum* (Bland, 1865) from the Ruby Mountains (Ports 1996), but it was not recorded elsewhere in state until this survey (Ports unpublished data; Pratt 1985).

PUNCTUM MINUTISSIMUM (I. LEA, 1841).—The Small Spot was found in 5 of the 12 habitat types in low numbers, making up approximately 2% of the total shells (Table 1). This species is found primarily in the eastern United States and Canada, although there are records from Idaho and Oregon (Pilsbry 1948), as well as from Montana (Hendricks 2012) and Wyoming (Beetle 1997). The populations surveyed in the park represent some of the first records of this species in the state, and since this survey it has been found in the Jarbidge Mountains, the Ruby Mountains (Nekola personal communication), and the Toiyabe Range of central Nevada (Fig. 2) (Ports unpublished data).

DISCUS WHITNEYI (NEWCOMB, 1864).—The Forest Disc was found in 7 of the 12 habitat types in low numbers, making up approximately 2% of the total shells (Table 1). This species has been recorded from the Spring Range of southern Nevada (Pratt 1985), the Ruby Mountains of northeastern Nevada (Ports 1996), and the mountains of central, northern, and western Nevada (Fig. 2) (Ports unpublished data). This species is found throughout the western United States and Canada, with one record from the White Pine Range (Pilsbry 1948). Pilsbry (1948) suggests that the scarcity of records for this species in Nevada is due to poor habitat availability; however, these more recent records confirm that *D. whitneyi* occurs in woodland habitats in several mountains and valleys of Nevada.

EUCONULUS FULVUS (MULLER, 1774).—The Bee Hive was found in 7 of the 12 habitat types in moderate numbers, making up 14% of the total shells (Table 1). In GBNP there exist 2 ecophenotypes of this species: a high dome-shaped shell with narrow whorls (large morph) and a lower spire form with rapidly expanding whorls (small morph). The small morph is found from the Spring Range in southern Nevada (Pratt 1985), north to the Ruby Mountains (Ports 1996) and the Jarbidge Mountains (Ports unpublished data) into central and western Nevada (Fig. 2) (Ports unpublished data). At this time the unusual high-domed morph has been found only in GBNP.

ZONITOIDES ARBOREUS (SAY, 1816).—The Quick Gloss was found in 8 of the 12 habitat types in low numbers, making up <1% of the total shells (Table 1). Pilsbry (1946) describes the range of this species as extending throughout the United States and Canada "except Nevada." The description by Pilsbry is due to the lack of recent records. Besides GBNP, this species occurs in the nearby Schell Creek Range, south to the Clover Range (Pratt 1985), into central Nevada, north to the Ruby and Jarbidge Mountains and in the Carson Range of western Nevada (Fig. 2) (Ports unpubl. data).

HAWAIIA MINUSCULA (A. BINNEY, 1841).—The Minute Gem was found in 3 of the 12 habitat types in low numbers, making up approximately 1% of the total shells (Table 1). This species was not recorded from Nevada by Pilsbry (1946); however, recent records show its presence in Oregon and Idaho (Frest and Johannes 2000, Burke 2013). More recent records from Nevada show it as present in the Snake Range, the Clover Range to the south, the Schell Creek Range, and the Quinn Canyon Range to the southwest (Fig. 2) (Pratt 1985). This species has been recorded from the Jarbidge Mountains in northern Nevada (Ports unpublished data) but not from the Ruby Mountains (Pratt 1985, Ports 1996). At this point it has not been recorded from central or western Nevada (Fig. 2) (Ports unpublished data).

VITRINA PELLUCIDA (MULLER, 1774).—The Western Glass Snail was found in 8 of the 12 habitat types in moderate numbers, making up approximately 11% of the total shells (Table 1). This species is found throughout the western United States and north into British Columbia, with 2 Nevada records from the White Pine Range and Spring Range (Fig. 2) (Pilsbry 1946). This species is common in the Ruby Mountains (Ports 1996) and is also found north to the Jarbidge Mountains and on the east slope of the Sierra Nevada (Carson Range) and central Nevada (Toiyabe Range) (Fig. 2) (Ports unpublished data).

DEROCERAS LAEVE (MULLER, 1774).—The Meadow Fieldslug was found in 2 of the 12 habitat types in low numbers, making up <1% of the total mollusks surveyed (Table 1). A Holarctic species, it may be the most widespread native slug in Nevada (Pilsbry 1948). It has been recorded from the Quinn Canyon Range and Clover Range of Nevada (Pratt 1985), as well as from the Ruby Mountains (Ports 1996) and the Schell Creek Range (Fig. 2) (Ports unpublished data).

Species Richness and Habitat Affinities

Species richness for land snails was highest in the xeric limestone/dolomite boulder and talus rockslides (II-15 species) and in the ephemeral riparian zones with limestone/dolomite rock (I-10 species), where percent total shells was 27% and percent total habitat was 34% (Table 1). Each of these habitat types contains an overstory of xeric woodlands, dominated by conifers such as Single-leaf pinyon pine (*Pinus monophylla*), ponderosa pine (*Pinus ponderosa*), Rocky Mountain white fir (*Abies concolor)*, Englemann spruce (*Picea engelmannii*), and Douglas-fir (*Pseudotsuga menziesii*), with patches of quaking aspen (*Populus tremuloides*) and deciduous shrubs (Sibley 2009). The lowest species diversity (VI-1 species) was recorded in a high-elevation bristlecone pine (*Pinus longaeva*) and common juniper (*Juniperus communis*) woodland that was also dominated by limestone and dolomite rock (Table 1). Species richness values in the perennial granite-quartzite riparian zones (III-12 species) and in the granite-quartzite rock and talus slides (IV-13 species) were relatively high, while habitat III supported twice the percentage of shells/habitat (18% vs. 9%) (Table 1). Habitat V was defined by narrowleaf cottonwood (*Populus angustifolia*), Gooding willow (*Salix goodingii*), grasses, and forbs with a granitic-schist gravel and perennial stream. Eight species were recorded in habitat V, which made up only 5% of the shells/habitat. Each of these habitats includes mesic woodlands dominated by conifers, patches of quaking aspen, cottonwood, willows, deciduous shrubs, grasses, and forbs with a perennial water source (Table 1). Habitats IX (perennial springs) and X (boggy streamsides) have the same species richness (11 species) and include the single species of slug *Deroceras laeve* and the succineid snail specific to these wet sites. The number of shells/habitat here are not comparable because the spring habitats were surveyed using hand collecting by minutes (Table 1). Habitats VII (bristlecone pine–common juniper woodland) and VIII (curl-leaf mountain mahogany [*Cercocarpus ledifolius*] and pinyon pine woodland) had a species richness of 3 and 4 with 1% and 2% shells/habitat, respectively (Table 1). Habitat XI included Wyoming sagebrush (*Artemisia tridentata*), rubber rabbitbrush (*Ericameria nauseosa*), and antelope bitterbrush (*Purshia tridentata*) steppe which supported 2 species (Perryman 2014), while habitat XII (pinyon pine and Utah juniper woodlands) had no shells in 8 soil/litter samples (Table 1).

DISCUSSION

Species Richness and Habitat Affinities

A total of 18 species of land snails and 1 species of slug were recorded in Great Basin National Park. Species richness and the percentage of total shells/habitat were uneven across the 12 habitat types described (Table 1). Generalist species include *Pupilla hebes, Vallonia cyclophorella, Euconulus fulvus,* and *Vitrina pellucida,* all of which had affinities for 7–9 of the 12 habitat types described. Only 2 species, a succineid snail and the slug *Deroceras laeve* were unique to 2 specific habitats (springs and boggy streamsides, habitats IX and X). Limestone/dolomite habitats (I and II) in GBNP supported abundant populations of small land snails represented by *P. hebes*, *V. cyclophorella, V. pellucida,* and *E. fulvus* (Table 1). Sixteen of the 18 species of land snails utilize limestone rock and talus habitats in the park. Beier et al. (2012) showed that land snail abundance and species diversity increased with limestone soils in northern hardwood forest. In GBNP, these habitats are associated with deciduous shrubs, aspen, and conifers. These sites may be critical to the survival and recolonization of adjacent woodland habitats after disturbances such as drought, wildfires, and livestock grazing (Boag 1985, Beetle 1997; Ports unpublished data).

In the eastern United States, land snail richness and abundance are greatest when snails are associated with carbonate cliffs (Nekola and Smith 1999). In GBNP there are several north-facing limestone cliff sites which support a high species richness and abundance of land snails. These sites are supported by deciduous shrubs growing at the base of the cliffs, providing a mesic microhabitat not only in GBNP but also in several Great Basin mountain ranges (Pratt 1985, Ports 1996, 2004; Ports unpublished data).

Granite/quartzite rock slides and perennial riparian zones (habitats III, IV, VII, and VIII) in GBNP support a high species diversity but a lower number of individuals (Table 1). The medium-size land snails represented by *Discus whitneyi*, *Zonitoides arboreus,* and *Microphysula ingersolli* were most common along the granite/quartzite perennial riparian zones but were also found in xeric, subalpine bristlecone pine and common juniper woodland (habitat VII) at 3185 m in granite/quartzite rock, an unusual rock type for bristlecone pine (Sibley 2009, Baker 2012). In the Ruby Mountains (Ports 1996) there are several perennial riparian zones of aspen/cottonwood habitats with a granitic/schist bedrock. This habitat affinity supports 14 species with a relatively large number of shells and shares 12 species with similar habitat affinities in GBNP (Ports 1996). This uncommon habitat affinity is found in several of the high-elevation metamorphic core complexes in the Great Basin, such as the Snake Range, Ruby Mountains, Toiyabe Mountains, Jarbidge Mountains, and Schell Creek Range (Fig. 2). Habitats of aspen/conifer woodlands found within the protection of deep canyons are critical for the maintenance of diverse land snail communities throughout the Great Basin, western United States, and Canada (Karlin 1961, Ports 1996, Beetle 1997, Nekola 2014).

In GBNP, the Mountainsnail *O. strigosa depressa* has an affinity for both granite/quartzite and limestone/dolomite rock slides and exists in limited isolated colonies. In GBNP, *O. hemphilli* and *O. nevadensis* appeared to be restricted to limestone/dolomite rock slides and ephemeral riparian zones with a limestone/dolomite substrate. Frest and Johannes (2000) and Burke (2013) list several species of *Oreohelix* from the Columbia Basin, Idaho, and Montana that are closely associated with metamorphic and igneous rock slides and talus; whereas in Nevada, Ports (2004) describes the use of both granite and limestone rock slides by *O. strigosa depressa* and the apparent dependence on limestone rock slides by *O. hemphilli, O. nevadensis,* and *O. loisae* (Ports 2004). Large land snails such as those in the genus *Oreohelix* have limited dispersal ability and are often endemic to local habitats and geographical regions such as mountains of the Great Basin (Chamberlin and Jones 1929, Ports 2004). The colonies of Mountainsnails in GBNP are primarily restricted to local microhabitats such as rock and talus slides or the base of limestone cliffs. Such local microhabitats are critical to the survival of these large land snails in GBNP, especially considering their limited dispersal ability and sensitivity to habitat disturbances such as livestock grazing and wildfires (Chang and Emberton 1993, Denmead et al. 2015).

In the northern Rocky Mountains of Montana, the highest elevations reported for *Z. arboreus, D. whitneyi,* and *M. ingersolli* range from 2300 to 2600 m, typically in mixed conifer/aspen woodland (Hendricks 2012). It is notable that these 3 species are sympatric in GBNP at a higher elevation (3000 m) in granite-quartzite rock type. In GBNP, *V. cyclophorella* was the only land snail recorded in a bristlecone pine–limber pine (*Pinus flexilis*) woodland (habitat VI) at 3000 m associated with the more typical limestone rock on the west side of the park (Baker 2012). A common species in Montana, *V. cyclophorella* is found up to 2300 m in mountain coniferous/aspen forest (Hendricks 2012).

Rock slides and talus slopes of both granite/quartzite and limestone/dolomite support the highest species richness in the park, providing multiple deep layers of rock, litter, and moist organic soils. Nekola (2003) found a thick leaf litter and deep organic soil layer with a high moisture content to be important conditions for land snail movement, avoidance of desiccation, and egg laying in the Great Lakes region. Rock slides, talus slopes, and cliff faces may act as similar refugia for many species of land snails in GBNP. Livestock grazing, wildfires, and drought cause populations of small land snails to be heavily impacted, reducing species richness and numbers (Chang and Emlen 1993). Specifically, livestock have been grazed in the riparian zones of the Snake Range from the late 1880s to 1986, when the region became a national park (Baker 2012), and experimental studies have shown that livestock trampling and removal of plant matter will result in loss of leaf litter and desiccation of soils, and will negatively impact land snail communities (Denmead et al. 2015). Rock slides and steep talus slopes are typically avoided by livestock, which prefer to graze in adjacent open woodlands along riparian zones and in adjacent shrublands (Fleichner 1994). The rock slides and talus slopes in the park may allow for maintenance of land snail populations and recolonization of rock slides and adjacent aspen/deciduous shrub woodlands (Boag 1985).

Beever et al. (2005) found significant vegetation changes in riparian vegetation in GBNP, including a lower cover of shrubs and forbs, a decrease in aspen coverage, and an increase in invasive communities of sagebrush steppe and pinyon pine/Utah juniper woodland. They attributed these changes to livestock grazing, wildfires, and specifically to periods of drought. In GBNP, the sagebrush-shrub steppe, making up approximately 15% of the plant communities (Beever et al. 2005), supported only 2 small species of land snails (*Pupilla hebes* and *Vallonia cyclophorella*). Pinyon pine and Utah juniper woodlands (approximately 10% of the plant communities) appeared not to support any mollusk species. In the Ruby Mountains, these 2 habitats held 4 and 2 species, respectively (Ports 1996). These 2 dominant habitats existing throughout the foothills of Nevada (Grayson 2011) typically support only 2–4 species of land snails (Pratt 1985; Ports personal observation). These habitat types are generally xeric year-round, experience long, cold winters, have a significant amount of bare ground, and exhibit poor litter/soil development, all of which probably inhibit colonization by land snails. The 2 small species of land snails found in the sagebrush steppe in GBNP were closely associated in dense litter beneath the deciduous shrubs such as bitter cherry (*Prunus emarginata*) and bitterbrush, but not beneath the dominant Wyoming big sagebrush and rubber rabbitbrush (Perryman 2014). A combination of the xeric characteristics of these 2 habitat types and the impact of livestock grazing may be factors limiting the ability of land snails to establish themselves within the sagebrush steppe and pinyon pine–Utah juniper woodlands of the Great Basin.

Biogeographical Patterns

The land snail communities found in the GBNP today with the highest species richness and highest number of shells are associated with rock and talus slopes of limestone and granite, along with mixed aspen/deciduous shrub/coniferous woodlands found in deep canyons. This habitat supports several species including *Pupilla hebes, Vallonia cyclophorella, Vitrina pellucida, Euconulus fulvus, Discus whitneyi, Zonitoides arboreus, Microphysula ingersolli, Vertigo modesta concinnula, Hawaiia minuscula,* and localized colonies of *Oreohelix strigosa depressa* and *Oreohelix hemphilli*. This land snail community is also found in other high-elevation metamorphic core complexes, including the Ruby Mountains of northeastern Nevada (Ports 1996), the Schell Creek Range just to the west of GBNP (Pratt 1985; Ports unpublished data), and the Deep Creek Range (Fig. 2) to the northeast of GBNP (Pratt 1985; Ports unpublished data). This land snail community, except for the absence of *Oreohelix hemphilli* and *O. nevadensis,* is found to make up a very similar land snail community in the canyons of the northern and central Wasatch Range (Chamberlain and Jones 1929, Nekola 2014), the Rocky Mountains of Montana (Hendricks 2012), and the Rocky Mountains of Colorado (Henderson 1931, Karlin 1961). Research into the past climatic changes of the Great Basin suggests that the pinyon pine and Utah juniper woodland did not exist during the Pleistocene Epoch, while a combination of Rocky Mountain conifers and sagebrush steppe dominated the lower to midelevations for approximately 1.5 Ma (Grayson 2011). Some species of land snails, such as *Vallonia cyclophorella, Pupilla hebes, Euconulus fulvus, Microphysula ingersolli, Vertigo modesta concinnula,* and the localized colonies of *Oreohelix* in GBNP may all represent relict populations that existed in lower elevations in plant communities such as sagebrush steppe and conifers with limestone rock slides.

Two species of mountainsnails collected in GBNP are represented by the 2 Nevada-endemic species *Oreohelix nevadensis* and *O. hemphilli*, which can be found in eastern and central Nevada. Pilsbry (1939) suggests that the shell characters of *O. nevadensis* resemble those of *O. haydeni hybrida* from the northern Wasatch Mountains of Utah. This resemblance in shell characters is also found in the taxon *O. loisae* from the Goshute Mountains of northeastern Nevada (Ports 2004) and in an undescribed species from the Cherry Creek Range in north central Nevada (Fig. 2) (Ports unpublished data). This genus is known for its large ecophenotypic variation in shell characters (Pilsbry 1939, Burke 2013), which makes it difficult to assign populations to specific taxa, except when such populations occur on isolated mountains such as the Snake Range and Goshute Mountains (Ports 2004). Populations of *Oreohelix hemphilli* in the GBNP and throughout its range of northern, eastern, and central Nevada are relatively consistent in their shells and genitalic characters (Ports 2004). These observations suggest that this species has its center of origin in the central Great Basin and is a possible example of an autochthonous endemic (Lomolino et al. 2006). A phylogenetic study for this species would allow a better understanding of its systematics and the closely related groups such as *Oreohelix handi* and *O. jaegeri* found in southern Nevada (Pratt 1985), *O. californica* in southern California (Pilsbry 1939) and the possibly disjunct species *O. eurekensis* from central Utah (Chamberlin and Jones 1929). Late Pleistocene middens (2–1.5 Ma) suggest that bristlecone pine, limber pine, and common juniper all existed as a plant community down to 1800 m in the Snake Range, north to the Goshute Mountains, and 60 km east of GBNP in the Confusion Range (Grayson 2011). Today in GBNP and in the Goshute Mountains, populations of *Oreohelix hemphilli* are found in such habitats at higher elevations above 2500 m (Ports 2004; Ports unpublished data) as these conifers shifted to higher elevations during the dry, warm Holocene period (1.4–0.5 Ma). There are relict populations of *O. hemphilli, Vallonia cyclophorella,* and *Pupilla hebes* in the Confusion Range (Fig. 2) at 1750 m, located in limestone talus within a pinyon pine and Utah juniper woodland (Ports unpublished data), where subalpine conifers such as bristlecone pine and limber pine survived until the late Pleistocene but are absent today (Grayson 2011).

Pratt (1985) recorded 10 species of land snails as well as the slug *Deroceras laeve* from the Snake Range including the GBNP. Species not previously recorded include *Gastrocopta pilsbryana,* a mountain species found in central (Quinn Canyon Range) and southern (Spring Range) Nevada (Fig. 2) but not found in northern or western mountains of the state (Pratt 1985, Ports 1996; Ports unpublished data). This species may have its most northern distribution in the GBNP, as it is recorded from the mountains of southern Utah and northern Arizona (Pilsbry 1948). The very small species *Paralaoma servilis, Punctum minutissimum,* and *Vertigo modesta concinnula* were not recorded by Pratt (1985) in the Snake Range but were recorded in this survey. This survey represents the first records for these 3 species in eastern Nevada, although the species have also been recorded from the Ruby Mountains (Ports 1996; Ports unpublished data). *Paralaoma servilis* (syn. *Punctum conspectum* Bland, 1865) is recorded from California, western Oregon and Washington, and through most of Idaho (Pilsbry 1939, Frest and Johannes 2000). *Punctum minutissimum* is generally found in the eastern United States and Canada but has also been recorded from northern Idaho and New Mexico (Pilsbry 1939, Frest and Johannes 2000). *Vertigo modesta concinnula* has been recorded from the southern Rocky Mountains of Utah, New Mexico, and Arizona (Nekola et al. 2018). The records of *Vallonia gracilicosta* from the park extend the range of this species into Nevada west of the Rocky Mountains of Colorado, Wyoming, Idaho, and Montana (Pilsbry 1948, Hendricks 2012). Pratt (1985) also did not record the land snails *Oreohelix nevadensis*, *Hawaii minuscula*, and the succineid land snail found in this survey.

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