

LAND SNAIL DIVERSITY IN WIND CAVE NATIONAL PARK, SOUTH DAKOTA

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ABSTRACT.—Eighty-two soil samples and additional hand-collection in Wind Cave National Park yielded over 2000 terrestrial gastropod specimens. The specimens represent 26 different species, including a South Dakota species of concern, *Vertigo arthuri*. New South Dakota state records for *Gastrocopta pellucida* and *Vertigo tridentata* were recorded. Samples from grassland habitats were less likely to contain snails and had lower species richness than samples from either forest or shrubland habitats. Canyons, creek beds, bases of limestone cliffs, and shrublands are important habitats for snails in the park.

Key words: land snails, South Dakota, national parks, gastropod, diversity.

Pilsbry (1948:978) commented that “the molluscan fauna of the upper Missouri valley still remain[s] almost unknown.” More than 50 years later, only a limited number of general works have been issued on terrestrial mollusks in the Great Plains (see Leonard 1959, and portions of Burch 1962, Hubricht 1985). In 1985, Hubricht still included South Dakota as one of the states most in need of snail surveys. Indeed, for the northern Great Plains, more questions remain than have been answered on molluscan diversity, distribution, taxonomy, and natural variation. The lack of information makes management and conservation efforts difficult. Although conservation priorities for land snails can be set using museum records alone (Heller and Safriel 1995), if few museum records exist for a region (such as the Black Hills), the priorities will be less reliable. The National Park Service’s Resource Challenge Initiative emphasizes the need to inventory natural resources in the national parks to better manage these resources (NPS 2000).

The purpose of this study was to survey land snail species at Wind Cave National Park (hereafter referred to as WCNP). A survey of snails in WCNP has not been conducted previously, although surveys have been conducted elsewhere in South Dakota (Henderson 1927, Jones 1932, Over 1942, Roscoe 1954, 1955), including other parts of the Black Hills (Frest and Johannes 2002, Jass et al. 2002). I sampled land snails in many WCNP vegetation com-

munities. Strong relationships between snails and vegetation communities have long been recognized (i.e., Shimek 1930, Burch 1956). Vegetation provides food and shelter for snails, and the structure and density of the vegetation determine thermal and moisture conditions for soil-dwelling species. This study provides information on land snail richness, distribution, and local habitat relationships in WCNP that may help improve land snail habitat conservation.

STUDY AREA

The Black Hills is a unique area biologically and geologically (Froiland 1999). It is 900 m to 1200 m higher than the surrounding Great Plains, and the area was not glaciated during the Pleistocene. The Black Hills also serves as a biological nexus where eastern, western, northern, and southern ranges of many organisms meet. A description of the wide variety of vegetation communities in the Black Hills can be found in Larson and Johnson (1999). Wind Cave National Park (WCNP) is located at the southern end of the Black Hills in southwestern South Dakota (Fig. 1). Famous for its underground wonders as home to the 6th largest cave in the world, WCNP also includes 11,454 ha of aboveground habitats, ranging from mixed grasslands to ponderosa pine (*Pinus ponderosa*) stands, to canyons in limestone and sandstone.

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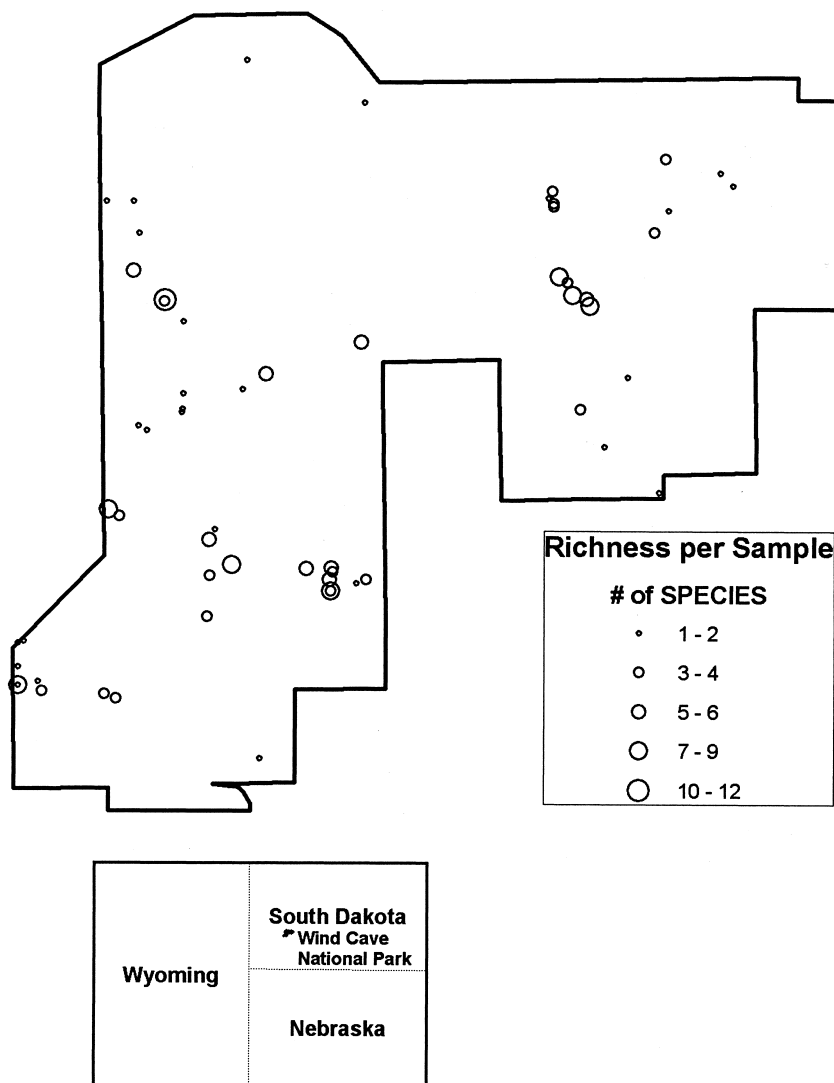


Fig. 1. Species richness varied across WCNP. Several locations (especially canyons/creekbeds) had high richness levels.

MATERIALS AND METHODS

Fieldwork was conducted in May and June 2002. Points for soil sampling were located in 27 different vegetation types (Table 1; as defined by park vegetation surveys and satellite mapping research of Cogan et al. 1999) to maximize the potential diversity of snails found. Three locations distributed around the park in each habitat type were sampled where possible. Specific locations of samples within these vegetation types were selected on the ground to maximize richness per sample. Maximizing richness by selecting likely microhabitats

has been used successfully in other studies (Emberton et al. 1996, Nekola 1999). In this study I took samples from moist areas with good litter cover or small, rocky debris, if such areas were available within the vegetation type. When vegetation types did not contain such microhabitats, I selected the sample location that was most representative of that vegetation type.

GPS locations (UTM coordinates, WGS 1984 Datum) of the sampling sites were recorded using Garmin (GPS 12XL) and Trimble (Geo-Explorer 3, version 1.04) units. GPS locations

TABLE 1. Habitats sampled in Wind Cave National Park. Vegetation classes are described by the dominant vegetation in that habitat class and were used for selecting sampling sites (Cogan et al. 1999). General habitat category refers to forest (F), grassland (G), or shrubland (S).

Vegetation class description	General habitat category (F,G,S)	No. of species identified
Purple three-awn/ fetid marigold herbaceous	G	0
Ponderosa pine on limestone cliff	F	11
Redbeds (silt/sandstone) with sparse vegetation	—	0
Little bluestem/ grama grass/ threadleaf sedge herbaceous with burned pine	F	7
Chokecherry shrubland with burned pine	S	5
Western wheatgrass/ Kentucky bluegrass complex with burned pine	G	3
Emergent wetland complex	—	2
Little bluestem/ grama grass/ threadleaf sedge herbaceous	G	2
Western wheatgrass/ Kentucky bluegrass complex	G	3
Introduced weedy graminoid herbaceous vegetation	G	3
Needle and thread/ blue grama/ threadleaf sedge herbaceous	G	1
Mountain mahogany/ side-oats grama shrubland (15%–50% cover)	S	8
Mountain mahogany/ side-oats grama shrubland (50%–100% cover)	S	11
Leadplant shrubland	S	4
Chokecherry shrubland	S	8
Snowberry shrubland	S	2
Creeping juniper/ little bluestem shrubland	S	8
Plains cottonwood/ western snowberry	F	5
Boxelder/ chokecherry	S	6
Bur oak stand	F	12
Green ash/ elm/ snowberry	F	7
Birch/ aspen stand	F	7
Ponderosa pine woodland complex I	F	0
Ponderosa pine/ little bluestem	F	8
Ponderosa pine/ chokecherry	F	2
Ponderosa pine woodland complex II	F	2
Young ponderosa pine dense cover	F	4

were used to create maps with ArcView software (version 8.2; ESRI 2001). At each sampling location, 3.8 L of soil and litter was collected from within a 0.25-m² quadrat. Soils were sifted through a sieve series (Newark and Hubbard brands), from 4 mm (#5 mesh size) to 0.25 mm (#60). Soil from each sieve layer was visually searched and any snails or shells were removed. Individual shells were examined under a microscope, counted, and identified to species where possible. In several samples, shells were broken or immature and could not be positively identified.

Additional locations along watersheds were searched visually for snails. At 6 of these locations, I also took canyon/creekbed soil samples for analysis. Two soil samples were also taken in a prairie dog (*Cynomys ludovicianus*) town after a prairie dog researcher reported finding shells in soil prairie dogs kicked out of their burrows.

The many different individual vegetation classes with few samples did not allow a robust analysis of vegetation versus snail presence.

Therefore vegetation classes were grouped into general habitat categories: grassland, shrubland, and forest. These general habitat categories were used to determine if a relationship existed between snail species richness or abundance among habitats.

RESULTS

I collected 82 soil samples, of which 59 contained snails and/or shells. An additional 6 areas were spot-searched for snails, and snails were found at 2 of these areas (Dry Creek and Cold Brook Canyon). Over 2000 whole and broken shells were examined, with 1738 identified to species. Live specimens were found at only 6 locations. Twenty-six different species were identified (Table 2). Specimens have been deposited at the Field Museum of Natural History in Chicago.

Species Descriptions

Identification of most species was fairly straightforward using Pilsbry (1946, 1948) and Burch (1962). Because live specimens were

TABLE 2. Land snail species and number of sites detected in WCNP, with taxonomy according to Turgeon et al. (1998), except as otherwise noted. Average per site refers to the average number of individuals in the samples where that species was found (i.e., includes only samples that contained that species). Habitat categories are F (forest), G (grassland), S (shrubland), and C (canyon/creek bed). Because canyons also may be somewhat forested, that category (C) is not distinct.

Species (common name)	Number of sites	Average per site	Habitat types (F,S,C)
<i>Catinella</i> sp.	13	3	F,S,C
<i>Cionella lubrica</i> (glossy pillar)	3	4	F
<i>Columella columella alticola</i> (mellow column)	2	3	F
<i>Deroceras laeve</i> (meadow slug)	2	2	C
<i>Discus catskillensis</i> (angular disc)	3	3	F
<i>Discus whitneyi</i> (forest disc)	5	8	F,C
<i>Euconulus fulvus</i> (brown hive)	13	8	F,G,S,C
<i>Gastrocopta armifera</i> (armed snaggletooth)	20	4	F,S
<i>Gastrocopta holzingeri</i> (lambda snaggletooth)	21	11	F,G,S,C
<i>Gastrocopta pellucida</i> (slim snaggletooth)	1	4	S
<i>Gastrocopta procera</i> (wing snaggletooth)	8	4	F,S
<i>Hawaiiia minuscula</i> (minute gem)	6	7	F,G,S,C
<i>Nesovitrea binneyana</i> (blue glass)	24	8	F,S,C
<i>Nesovitrea electrina</i> (amber glass)	1	5	F
<i>Pupilla blandi</i> (Rocky Mountain column)	3	5	S,C
<i>Pupilla hebes</i> (crestless column)	1	32	F
<i>Pupilla muscorum</i> (widespread column)	13	2	F,G,S,C
<i>Pupoides albilabris</i> (white-lip dagger)	5	2	F,G,S
<i>Striatura milium</i> (fine-ribbed striate)	1	2	F
<i>Vallonia gracilicosta</i> (multirib vallonina)	35	17	F,G,S,C
<i>Vallonia parvula</i> (trumpet vallonina)	11	15	F,G,S,C
<i>Vallonia pulchella</i> (lovely vallonina)	7	9	F,S
<i>Vertigo arthuria</i> ^a	2	4	F,S
<i>Vertigo tridentata</i> (honey vertigo)	1	1	F
<i>Vitrina alaskana</i> ^b	4	6	F,S,C
<i>Zonitoides arboreus</i> (quick gloss)	2	1	S,C

^aNo common name is listed in Turgeon et al. (1998).

^bTurgeon et al. (1998) list *Vitrina pellucida* as the "western glass-snail." However, Pilsbry (1946) considered South Dakota specimens to be *V. alaskana*, and that convention is followed here.

not available for most species (see below for discussion of the lack of living specimens), shell characters alone were used for identification. Scientific names from this study follow Turgeon et al. (1998). A few points to note on the identifications are explored here.

CATINELLA.—Specimens in the genus *Catinella* were not assigned to species level. Succineids (including *Catinella*, *Oxyloma*, and *Succinea*) have few shell characteristics that can be used for identification purposes. The specimens in this study were assigned to the genus *Catinella* based on work by Burch (1962:67) that describes *Catinella* with a "shell relatively small, generally 11 mm or less in length, dull; spire long, almost as long as the shell aperture." Frest and Johannes (2002:70) state that "shell characters of *Catinella gelida* are sufficiently distinctive as to make it unlikely to be confused with other described North American succineids." In contrast, others have cautioned against the use of shell characters alone in

assigning succineids to species (Burch 1962, Hoagland and Davis 1987). Since no living specimens of *Catinella* were found, the WCNP samples could not confidently be assigned to a particular species.

COLUMELLA.—Specimens tended to be cylindrical as is the *Columella columella alticola* pictured in Jass et al. (2002), and they are therefore identified as such. The only *Columella* species Frest and Johannes (2002) identified was *C. simplex*, which narrows at the top of the shell. It remains unclear whether the 2 species reside in different portions of the Black Hills, or if the WCNP specimens show different variation in shape than the Frest and Johannes (2002) specimens.

GASTROCOPTA.—Several *Gastrocopta* species were identified. All except *Gastrocopta pellucida* had been reported previously from South Dakota. *Gastrocopta pellucida* is distinguished from other *Gastrocopta* by its narrow diameter, tooth structure, and thin lip (Pilsbry 1948,

TABLE 3. Comparison of WCNP gastropod species found in studies from the Black Hills and western South Dakota.

Species	Current study	Frest and Johannes (2002)	Jass et al. (2002)	Over (1942) ^a	Roscoe (1954, 1956) ^a
<i>Anguispira alternata</i>					x
<i>Arion fasciatus</i>		x			
<i>Carychium exiguum</i>		x		x	x
<i>Carychium exile</i>				x	x
<i>Catinella</i> sp.	x		x		
<i>Catinella gelida</i>		x			
<i>Cionella lubrica</i>	x	x ^c		x	x
<i>Columella columella alticola</i>			x		
<i>Columella simplex</i>		x	x		
<i>Deroceras laeve</i>	x	x	x	x	x
<i>Discus catskillensis</i>	x				x
<i>Discus whitneyi</i>	x	x	x		x
<i>Discus shimeki</i>		x			x
<i>Euconulus fulvus</i>	x	x		x	x
<i>Gastrocopta agna</i>				x	
<i>Gastrocopta armifera</i>	x	x	x	x	x
<i>Gastrocopta clappi</i>				x	
<i>Gastrocopta contracta</i>				x	x
<i>Gastrocopta holzingeri</i>	x	x		x	x
<i>Gastrocopta pentodon</i>		x		x	x
<i>Gastrocopta pellucida</i>	x				
<i>Gastrocopta procera</i>	x	x	x	x	x
<i>Gastrocopta tappamiana</i>				x	x
<i>Helicodiscus eigenmanni</i>					x
<i>Helicodiscus parallelus</i>				x	x
<i>Helicodiscus singleyanus</i>					x
<i>Hawaiiia minuscula</i>	x	x	x		x
<i>Limax maximus</i>		x			
<i>Nesovitrea binneyana</i>	x	x			x
<i>Nesovitrea electrina</i>	x				x
<i>Oreohelix cooperi</i>		x		x	x
<i>Polita hammonis</i> ^b				x	
<i>Polygyra monodon</i>				x	
<i>Punctum pygmaeum</i>				x	
<i>Punctum minutissimum</i>		x			x
<i>Punctum californicum</i>				x	x
<i>Pupilla blandi</i>	x	x		x	x
<i>Pupilla hebes</i>	x		x		
<i>Pupilla muscorum</i>	x		x	x	
<i>Pupilla syngenes</i>					x

Burch 1962). The previously reported range included Florida west to California with reports as far north as Colorado and isolated locations in New Jersey and Maryland (Pilsbry 1948, Burch 1962, Hubricht 1985).

PUPILLA.—Two of the *Pupilla* species identified in this study, *P. hebes* and *P. muscorum*, were also found by Jass et al. (2002). The 3rd, *P. blandi*, was the only *Pupilla* found by Frest and Johannes (2002). Further analysis is needed to determine whether these species are restricted to different portions of the Black Hills.

VALLONIA.—The main shell characteristics used to define differences in *Vallonia* species include shell diameter, umbilicus diameter,

and number of ribs on the shell (see Burch 1962). However, the specimens from this survey did not neatly fit in the defined categories, generally having rib numbers within the range for multiple species. Frest and Johannes (2002) include 3 ribbed *Vallonia* species—*V. gracilicosta*, *V. cyclophorella*, and *V. perspectiva*—in their report from the Black Hills. However, a recent revision of the genus *Vallonia*, which includes specimens from all over the world, found considerable variability within Rocky Mountain populations of *V. gracilicosta* (Gerber 1996). For the purposes of this study, larger specimens (>2 mm) were considered *V. gracilicosta*, while smaller specimens (<2 mm)

TABLE 3. Continued.

Species	Current study	Frest and Johannes (2002)	Jass et al. (2002)	Over (1942) ^a	Roscoe (1954, 1956) ^a
<i>Pupoides albilabris</i>	x	x	x	x	x
<i>Pupoides inornatus</i>				x	x
<i>Stenotrema leai</i>					x
<i>Striatura milium</i>	x	x			
<i>Strobilops labyrinthica</i>		x			
<i>Succinea avara</i>				x	x
<i>Succinea grosvenorii</i>				x	x
<i>Succinea haydeni</i>				x	x
<i>Succinea higginsii</i>				x	x
<i>Succinea indiana</i>		x			
<i>Succinea nuttalliana</i>				x	x
<i>Succinea ovalis</i>					x
<i>Succinea stretchiana</i>		x			
<i>Vallonia albula</i>					x
<i>Vallonia costata</i>				x	x
<i>Vallonia cyclophorella</i>		x	x		x
<i>Vallonia gracilicosta</i>	x	x	x	x	x
<i>Vallonia parvula</i>	x			x	x
<i>Vallonia perspectiva</i>		x		x	x
<i>Vallonia pulchella</i>	x	x		x	x
<i>Vertigo arthuri</i>	x	x			
<i>Vertigo concinula</i>					x
<i>Vertigo elatior</i>		x			
<i>Vertigo gouldi</i>			x		
<i>Vertigo milium</i>				x	x
<i>Vertigo modesta</i>		x	x		
<i>Vertigo ovata</i>				x	x
<i>Vertigo paradoxa</i>		x			
<i>Vertigo tridentata</i>	x				
<i>Vitrina alaskana/pellucida</i> ^d	x	x		x	x
<i>Zoogenetes harpa</i>		x			
<i>Zonitoides arboreus</i>	x	x	x	x	x
<i>Zonitoides minuscula</i>				x	
<i>Zonitoides nitida</i>				x	x
<i>Zonitoides singleyana</i>				x	

^aThese studies report species from areas of eastern South Dakota as well.

^bThe identity of Over's (1942) *Polita hammonis* is unclear. *Polita* was a former name for *Oxychilus*, but the only *hammonis* in the Zonitinae recorded in Pilsbry is a species of *Nesocitrea*. Over (1942) may have been referring to *Nesocitrea electrina* or *N. binneyana*.

^cFrest and Johannes refer to their specimens as *Choclicopa lubricella*. *Choclicopa* is considered a synonym of *Cionella* (Pilsbry 1948, Turgeon et al. 1998). Turgeon et al. (1998) state that *C. lubrica* is the only species found in North America. Hubricht (1985) recognizes both species, but offers no distinction between them. For the purposes of this table, they are considered the same entity.

^dOnly *Vitrina pellucida* is recognized by Turgeon et al. (1998). Other sources mention only *V. alaskana* in the western U.S. (Hubricht 1985). Pilsbry (1946:502) states that *V. alaskana* is distinct from the European *V. pellucida*.

were considered *V. parvula*. These assignments follow Burch (1962), but a more conservative assignment would be to consider all *Vallonia* specimens as *V. gracilicosta*.

Vallonia pulchella has no ribs and so should be easy to distinguish from other *Vallonia*. However, in the current study, ribs on a few older *Vallonia* specimens were wearing off, which could result in worn shells being incorrectly identified. In this study specimens with no sign of ribs were considered to be *V. pulchella*.

VERTIGO.—Two *Vertigo* species were found: *V. arthuri* and *V. tridentata*. These species are differentiated by the number and position of

the teeth (Pilsbry 1948). *Vertigo arthuri* is a species whose distribution is not fully understood. Originally it was recognized only from North Dakota (Pilsbry 1948). It had been previously identified in the Black Hills by Frest and Johannes (2002) and has been recently reported by Nekola (2002) from upper Midwest locations.

Vertigo tridentata, with only 3 teeth, was not previously reported from South Dakota. The previously recognized range for *V. tridentata* stretched from Maine south to Tennessee in the east and Minnesota south to Texas in the west (Pilsbry 1948, Burch 1962, Hubricht 1985).

Richness and Habitat Characteristics

Individual soil samples contained from 0 to 210 shells. WCNF contains 35% of the land snail diversity known for western South Dakota (Table 3). On average, samples with snails contained 29 individuals of 3 different species. Sixty-three samples from WCNF contained 3 or fewer species. Common species dominated the samples, with just 5 species (*Vallonia gracilicosta*, *Gastrocopta holzingeri*, *Nesovitrea binneyana*, *Vallonia parvula*, and *Euconulus fulvus*) accounting for 75% of the individuals identified.

Snail shells were found in at least 1 sample from all surveyed vegetation types except purple three-awn/fetid marigold herbaceous community and redbeds (silt/sandstone) with sparse vegetation. Chi-square analyses showed that general habitat categories (forest, grassland, shrubland) were significantly different in the number of sites where snails were present. Samples from grassland habitats were more likely to contain no snails.

Species richness also varied across the landscape (Fig. 1), but the highest levels appear centered along creek beds in canyons. Species richness was also lower in grassland habitats than in either forests or shrubland habitats.

A few species were associated with a particular habitat category or categories. Table 2 shows associations between snail species and their preferred habitats. *Cionella lubrica* and *Columella columella alticola* were found only in forested habitat. *Deroceras laeve* was found only in canyons or along creek beds. *Nesovitrea binneyana* was more abundant in forests than in either grasslands or shrublands, although it was present in all habitats. *Gastrocopta armifera* was equally abundant in shrublands and forests. Other species tested showed no difference in abundance among habitat types.

DISCUSSION

Comparison of Species List with Other Studies

The species found in this study are similar to those found in other studies in the region (i.e., Over 1942, Roscoe 1954, 1955, Frest and Johannes 2002, Jass et al. 2002; Table 3). Two species reported here, *Gastrocopta pellucida* and *Vertigo tridentata*, were not reported in

earlier studies. Both were rare in WCNF, with only a single location each.

Notably absent from WCNF are specimens of *Oreohelix*. Although fairly common on shaded talus slopes in more northern areas of the Black Hills, *Oreohelix* becomes less frequent in the central and southern areas of the Black Hills (Frest and Johannes 2002). Jass et al. (2002) also did not find any evidence of *Oreohelix* in their study, which included the extreme southern Black Hills. The southern extent of the Black Hills differs in soil type, geology, moisture, and number of deciduous trees (Froiland 1999). Any or all of these factors may contribute to slight differences in snail communities.

The South Dakota Department of Game, Fish and Parks includes 5 gastropods among their rare species: *Vertigo arthuri*, *Vertigo paradoxo*, *Discus shimekii*, *Catinella gelida*, and *Oreohelix strigosa cooperi* (SDDGFP 2001). *Vertigo arthuri* was found in WCNF. The *Catinella* specimens found here may be *C. gelida* but cannot be confidently assigned to species without analysis of internal anatomy. The other 3 species were not found in WCNF, although they have been reported elsewhere in the Black Hills (Frest and Johannes 2002).

Species Richness

A previous Black Hills study reported 0 to 17 species per site with an average of 4.3 when only sites with snails present were included (Frest and Johannes 2002). A few species (*Discus whitneyi*, *Zonitoides arboreus*, *Euconulus fulvus*, *Nesovitrea binneyana*, and *Vitrina pellucida*) also dominated Frest and Johannes's (2002) study. Their reported dominance is based on occurrence, not abundance, since they did not count all individuals. Nevertheless, the frequency of *D. whitneyi*, *Z. arboreus*, and *V. pellucida* is interesting since these species were relatively rare at WCNF. This may be attributable to site selection because Frest and James (2002) focused on moister habitats and talus slopes, which are rare in WCNF, rather than more evenly sampling across all vegetation types.

Species richness in the Black Hills is not unlike results from Beetle's (1997) study in Yellowstone aspen stands, which reported 3 to 5 snails per stand. These stands were studied after a wildfire burned the area. Richness increased to 11 species in a "damp site . . . [with]

favorable litter, soil, and moisture” (Beetle 1997:8).

Studies from other regions have reported even higher levels of species richness. In Wisconsin, 1-m² quadrats averaged 6.6 species (Nekola and Smith 1999). A study including sites across the Great Lakes region found 11% of samples contained 24 or more species (Nekola 1999). These observed richness numbers are far below the 61 species · km⁻² reported from a tropical rainforest in Malaysian Borneo (Schilthuizen and Rutjes 2001). Emberton (1995) reported that the highest diversity of terrestrial gastropods in the United States was 44 species in <4 ha found by Leslie Hubricht in the mountains of Kentucky. Coniferous forests and grasslands are expected to have lower diversities of land snails than other habitat types (Solem 1984).

Observed numbers per sample (Table 2) are also lower than in other studies. Van Es and Boag (1981) found an average of 11.6 *Vitrina alaskana*, 48.9 *Discus whitneyi*, and 27.3 *Euconulus fulvus* per sample. It is not clear whether their litter samples from 0.5-m² areas in size represent the same volume of soil as in the WCNP study. Because their study also occurred in a forest in Alberta with abundant deciduous trees (*Populus* spp.), it is expected that more snails would be present.

Few Living Specimens

The low number of living specimens collected in WCNP cannot be easily explained. Frest and Johannes (2002) do not indicate what percentage of their findings were alive but suggest that living snails were commonly observed. Emberton et al. (1996) found soil samples had fewer live samples than other sampling methods, but they reported living representatives of 28% of snail species in soil samples.

One potential explanation for the low number of live specimens is a possible die-off of snails. One of the main factors in snail death is dessication (Solem 1984). Snail populations may fluctuate with environmental stress, and since WCNP has been under drought conditions for the past few years, it is likely many snails have died. Another explanation is that shells collected are only remains from a time period when the habitat was more suitable for snails. Pearce (2002, personal communication) found that shells in eastern forests exist in the soil about 30 years before completely decaying.

Shells in the drier climates of the Great Plains likely persist slightly longer, but even so, shells recovered in this study must represent snails that were alive within the recent past. A 3rd explanation is that during these unfavorable drought conditions, snails in WCNP have sought refuge in areas not sampled. Unfortunately, these hypotheses cannot be tested with the available data.

Size of Specimens

Several species of WCNP land snails were smaller in size than reported in previous descriptions. *Cionella lubrica* was 2.8 mm tall and had only 4 whorls although they are listed in Pilsbry (1948) as being 5–6.5 mm and having 5.5 to 6 whorls. *Vitrina alaskana* specimens ranged from 2.3 mm to 3.8 mm in diameter, although Pilsbry (1946) described them as 5 mm or larger. WCNP snails were only slightly smaller than those in Alberta aspen/poplar forests (Van Es and Boag 1981). For example, their *Vitrina alaskana* specimens averaged 4.35 mm ($n = 152$). Pilsbry (1948:932) discussed a small form of *Pupilla blandi* east of the Rocky Mountains, adding that “it is probably a ‘hunger form’ occupying arid situations.” Since this phenomenon was observed in several species, WCNP may not be optimal for maximizing growth.

Habitat Type

Seven generalist species (*Euconulus fulvus*, *Gastrocopta holzingeri*, *Hawailia minuscula*, *Pupilla muscorum*, *Pupoides albilabris*, *Vallonia gracilicosta*, and *Vallonia parvula*) were found in all habitats (Table 2), while other species were more specialized. For example, *Deroceras laeve* was found only in canyon/creek bed areas. *Cionella lubrica* and *Columella columella* were only in forest habitat. *Nesovitrea binneyana* was more abundant in forested habitat. *Gastrocopta pellucida* was found only at 1 site in shrubland. *Nesovitrea electrina*, *Striatura milium*, and *Pupilla hebes* were also only at 1 location. *Discus catskillensis* may prefer forested habitat, although it was also found in a wetland sample.

Some shrubland areas were also important snail habitats at WCNP. Six of the 12 samples from mountain mahogany (*Cercocarpus montanus*), chokecherry (*Prunus virginiana*), and creeping juniper (*Juniperus horizontalis*) sites had species richnesses of 5 or higher.

No species were found only in grasslands, in contrast to the ordination analyses of Nekola (2003) that showed many snail species, including several found at WCNP (*Cochlicopa lubrica*, *Discus whitneyi*, *Nesovitrea electrina*, *Gastrocopta armifera*, *Gastrocopta procera*, *Pupilla muscorum*, *Pupoides albilabris*, *Vallonia parvula*, and *Vallonia pulchella*) appeared to be grassland specialists. Nekola incorporated more samples across a much larger spatial scale which gives his results more credence. However, because the grasslands of the Great Lakes region of Nekola's study are moister than the arid region of western South Dakota, those grasslands may be able to support more species. Nekola apparently did not sample shrubland, which may have influenced the preferences shown at WCNP.

Earlier studies questioned whether snails occupy coniferous forests in western North America. Karlin's (1961) surveys across Montana, Colorado, and New Mexico reported that 99% of snails occurred within forests where deciduous trees were a significant component. Kralka (1986) also found most snail species preferred areas dominated by deciduous vegetation in Alberta, Canada. He did note that *Vertigo gouldi* preferred coniferous habitats. WCNP data and those of Frest and Johannes (2002) contradict those findings, since most WCNP forest sites are dominated by ponderosa pine. Locasciulli and Boag (1987) also found the highest densities of snails in coniferous forests in Alberta. Although the most diverse (12 species) location in WCNP was a stand of bur oak, *Quercus macrocarpa*, a cliff site dominated by ponderosa pine had 7 species. Carbonate cliffs and canyons often provide important habitats for snails (Beetle 1989, Nekola and Smith 1999). Two samples along Dry Creek contained over 300 individuals and 11 species total. In WCNP these areas tend to have calcareous soils (Ensz 1990, Ford 2002).

CONCLUSIONS

WCNP supports a relatively high diversity of land snails, with 35% of the regional species represented. Recent droughts have probably affected snail populations in the park, based on the large number of empty shells found in this study. Riparian areas (especially Dry Creek and Cold Creek), shrubland, and limestone cliffs are especially important for WCNP snail diversity and should be managed with care.

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