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Occurrence of North American porcupine (*Erethizon dorsatum*) in the Black Hills, South Dakota

Lenora M. Dombro[1], Earl Perez-Foust[2], Daniel Roddy[2], Daryl E. Mergen[3], and Robert A. Gitzen[4,*]

[1]*Custer Gallatin National Forest, Ashland Ranger District, Ashland, MT 59003*
[2]*Wind Cave National Park, Hot Springs, SD 57747*
[3]*Mergen Ecological Delineations, Inc., Colorado Springs, CO 80905*
[4]*School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849*

Abstract.—During the twentieth century, the North American porcupine (*Erethizon dorsatum*) was common in the Black Hills of western South Dakota and northeastern Wyoming. However, the low number of recent observations in the region has led to concern that porcupine populations have declined. We conducted systematic surveys to assess porcupine occurrence at two hundred and sixty-three 1-ha sites in the Black Hills National Forest, Custer State Park, Jewel Cave National Monument, Mount Rushmore National Memorial, and Wind Cave National Park during 2016–2017. We observed no porcupines or recent feeding sign. We also noted few recent observations in information compiled from online databases and from other natural resource surveys with which we have been involved in the South Dakota Black Hills. Given the apparent abundance of porcupines in this area in the twentieth century, our results suggest that populations have declined dramatically. Predation by mountain lions (*Puma concolor*), habitat loss, and human-caused mortality are potential contributing factors, but estimating the degree of population declines and assessing hypotheses about the causes are hindered by a lack of long-term data on the region's porcupine populations. Moreover, accounts of the region's mammalian fauna suggest that porcupines were not abundant in the region during the late 1800s but became common in the early twentieth century.

Resumen.—Durante el siglo XX, el ursón o puerco espín norteamericano (*Erethizon dorsatum*) se encontraba comúnmente en las Colinas Negras del lado occidental de Dakota del Sur y noreste de Wyoming. Sin embargo, a causa del escaso número de observaciones en la región recientemente ha surgido una preocupación sobre la disminución de la población del puerco espín. Realizamos estudios sistemáticos para evaluar las apariciones del puerco espín en doscientos sesenta y tres sitios de una hectárea en el Bosque Nacional Black Hills, el Parque Estatal Custer, el Monumento Nacional Jewel Cave, el Monumento Nacional Monte Rushmore y el Parque Nacional Wind Cave, durante los años 2016–2017. No observamos ningún puerco espín ni signos de alimentación recientes. Al igual, notamos muy pocas observaciones en la información compilada de las bases de datos en línea y de otros estudios de recursos naturales en los que hemos estado involucrados en las Colinas Negras en Dakota del Sur. Dado que la población del puerco espín era abundante en el siglo XX en el área de estudio, nuestros resultados indican que la población ha disminuido de forma dramática. Las posibles causas que han contribuido a esto incluyen la depredación de los pumas (*Puma concolor*), la pérdida de hábitat y la mortalidad causada por el ser humano. Sin embargo, estimar el grado de disminución en la población y evaluar las hipótesis con respecto a las causas, es difícil por la falta de datos a largo plazo de la población de puerco espín en la región. Además, información sobre la fauna mamífera en la región indica que el puerco espín no tenía una población abundante a finales del siglo XIX, sino que fueron más comes a principios del siglo XX.

The Black Hills region is an isolated uplift in western South Dakota and northeastern Wyoming that rises to 1300 m above adjacent grasslands (Froiland 1990). During the twentieth century, the North American porcupine (*Erethizon dorsatum*; hereafter "porcupine") was a common mammal in the Black Hills (Turner 1974, Froiland 1990). In 1914, the acting superintendent of the nascent Wind Cave National Park (WICA) in the southern Black Hills observed that the porcupine was "present in such numbers as to be a menace to the pine timber. This animal is destroying large numbers of the younger pines" (Boland 1913; see also Dille 1914). The forest supervisor of the Black Hills National Forest (BHNF)

*Corresponding author: rag0012@auburn.edu

reported that in 1933 the Civilian Conservation Corps treated 28,000 acres of forestland with poisoning "to kill porcupines and other rodents" (Krueger 1934:12). Localized poisoning to reduce damage in research plots of the Black Hills Experimental Forest of the BHNF continued until circa 1980 (H. Messner personal communication). In describing the effectiveness of roadside spotlight surveys combined with clubbing for killing porcupines, Spencer (1950) reported that in the fall of 1949, a U.S. Forest Service biologist and an associate "averaged some forty porcupines a night (to midnight only) along roads on the Harney National Forest" (now part of the Black Hills National Forest). Van Deusen and Myers (1962) reported that of the 7400 immature ponderosa pines (*Pinus ponderosa*) that were measured on 56 plots across the BHNF, nearly 10% had porcupine damage. Foresters continued to consider the porcupine a significant agent of damage in young pine stands through the 1970s (Boldt and Van Deusen 1974). As recently as the late 1990s, WICA maintenance staff placed metal flashing around trees at the park's visitor center to reduce porcupine damage (D. Roddy personal observation).

However, there is concern that porcupine populations have declined in the South Dakota Black Hills (hereafter, SD Black Hills). In WICA, informal observations by long-term staff suggest that porcupine populations have decreased dramatically in recent decades (Komp et al. 2011). Our initial discussions with state and federal natural resources personnel in the SD Black Hills indicated that sightings of porcupines or their sign have become very uncommon in many areas. Yet, there is high uncertainty about trends in the area's porcupine populations, because most information about past and current abundance is anecdotal or qualitative. Our objectives were to assess the current occurrence of porcupines in the SD Black Hills and to provide a baseline for assessing potential future changes in occurrence. To assess current status, we used data from systematic surveys in selected management units along with opportunistic information from natural resources surveys that focused on other taxa in the region.

We conducted systematic surveys at 5 management units within the Black Hills (Fig. 1): the Black Hills Experimental Forest (BHEF), Custer State Park (CSP), Jewel Cave National Monument (JECA), Mount Rushmore National Memorial (MORU), and Wind Cave National Park (WICA). Within each management unit, we used simple random sampling in ArcGIS (ESRI 2012) to select 1-ha (100 m $\times$ 100 m) survey sites from the sample frame of all potential sites in each unit. We excluded inaccessible areas (e.g., cliff areas) and developed areas identifiable within map layers. In addition, we field-validated all sites and eliminated 9 sites from the CSP sample that met our exclusion criteria. Final number of surveyed sites varied with management unit size and prevalence of inaccessible areas, with maximum absolute sample sizes at CSP and WICA kept at $\leq$100 sites for feasibility (BHEF: management unit area 1391 ha, 45 sites sampled; CSP: 28,733 ha, 100 sites; JECA: 515 ha, 15 sites; MORU: 518 ha, 23 sites; WICA: 11,451 ha, 80 sites). Because porcupines can occur frequently in woody draws, shrublands, and grasslands interspersed with woody cover types (Higgins et al. 2000), we retained nonforested areas for sampling.

We surveyed each sample site once during December 2016 to November 2017 for evidence of porcupine presence. During each survey, a single observer walked the site periphery and within the site interior, looking for porcupines and feeding sign. Feeding sign was defined as a patchwork of bark that was removed by porcupines, often in a rounded or oval shape and showing marks from incisors (Spencer 1964, Klvana et al. 2004). We distinguished porcupine sign from scrapes caused by elk (*Cervus elaphus*; nomenclature follows Bradley et al. 2014), deer (*Odocoileus hemionus* and *O. virginianus*), or American bison (*Bos bison*), based on porcupine sign often being higher in trees, being cleaner, and having no hanging bark (Elbroch 2003). We categorized porcupine feeding sign as recent (light-colored with sap protruding, surrounded by lighter-colored bark, bark chips potentially still present on the ground) or older (gray or brown with bark noticeably recovering on the edges and no fresh sap, likely > 3–5 years old) (Elbroch 2003).

We recorded no porcupine sightings or recent sign in any of the 263 sites surveyed across the 5 management units. Older sign was observed at a low number of sites in most units (BHEF: 2 sites; CSP: 1 site; JECA: 0 sites; MORU: 2 sites; WICA: 10 sites). Most survey sites (82% overall) were in ponderosa

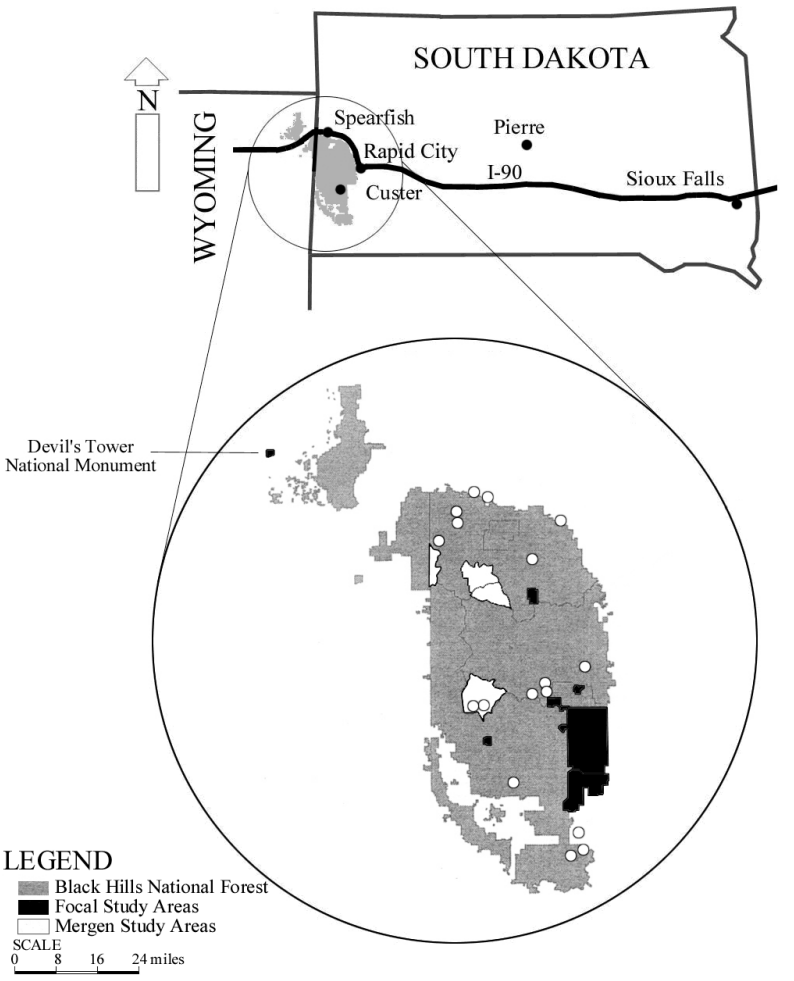

Fig. 1. Survey areas for assessing occurrence of North American porcupine (*Erethizon dorsatum*) in the South Dakota Black Hills region, 2017–2018. Devil's Tower National Monument and selected cities are shown for reference.

pine stands. Other forested sites included hardwood-dominated woody draws and riparian areas. Nonforested sites included grasslands, black-tailed prairie dog (*Cynomys ludovicianus*) colonies, burned snag stands, and grassland mixed with sparse ponderosa pine; percentages of sample sites in nonforested types were 0% for BHEF and MORU, 15% for CSP, 13.3% for JECA, and 38.8% for WICA.

During other recent natural resources surveys in some of these units, we observed little or no recent evidence of porcupines. No porcupines were observed during annual 2007–2017 spotlight surveys (about 80–90 nights per year) for black-footed ferrets (*Mustela nigripes*) at WICA and CSP (D. Roddy unpublished data). During our 2016–2017 study, WICA staff reported a sighting of a live porcupine at the visitor center parking lot. During field surveys for smaller rodents at MORU in summer and fall 2010 and 2012, no porcupines were observed during several hundred crew-days per year while we accessed about one hundred 0.36-ha survey sites across the memorial for small mammal trapping and midden surveys. The only evidence of porcupines noted at MORU was localized feeding damage in one patch of pine saplings (R. Gitzen unpublished data). For comparison with these encounter rates, Stebler (1939) collected 2 porcupines in 18 days of mammal surveys in the central Black Hills.

During 2002–2016, D. Mergen conducted 590 days of botanical field surveys at a rate of 40–120 ha per day throughout the BHNF. Mergen's only recollection of any porcupine observations during this time was of one dead animal. Starting in 2016, he and another botanist explicitly recorded porcupine observations during similar vegetation surveys across the SD Black Hills. During approximately 100 more "person field days" in 2016–2018, they inventoried 12 SD Game Production Areas (7780 ha), sampled 41 different aspen (*Populus tremuloides*) sites (2–4 ha per site; including 11 sites within CSP), and surveyed 17,042 ha for weeds within the northern SD Black Hills. The weed surveys included areas where Mergen had observed numerous porcupines during 1973–1977 as a Black Hills resident. Their only porcupine observations during 2016–2018 were of 2 dead porcupines in Game Production Areas inventories.

Consistent with our lack of observations, other natural resources personnel of CSP, JECA, MORU, and WICA indicated in conversations with us that they had not seen porcupines in recent years. The iNaturalist citizen-science database (iNaturalist 2019) contained only one porcupine observation for the SD Black Hills as of December 2019; the observation was from 2002 at WICA. For comparison, numerous "research grade" observations for this area during 2010–2018 had been submitted for other noncryptic and arguably noncharismatic terrestrial rodents, including North American red squirrels (*Tamiasciurus hudsonicus*; 21 observations), least chipmunks (*Tamias minimus*; 27 observations) and yellow-bellied marmots (*Marmota flaviventris*; 17 observations). Following Appel et al. (2017), we also searched the Flickr photograph repository (www.flickr.com; key words: "Black Hills AND porcupine", "South Dakota AND porcupine"; date of search: 26 December 2019), with the only photographs of wild porcupines in the SD Black Hills being of a single dead porcupine in the central Black Hills. In contrast, there were ~10 photographs of yellow-bellied marmots from the Black Hills. Also following Appel et al. (2017), we searched the Global Biodiversity Information Facility (GBIF 2019), locating no additional twenty-first-century specimen records for porcupine in the SD Black Hills.

Collectively, these survey results and supplemental observations indicate current low occurrence or absence of porcupines both in our focal management units and across much of the Black Hills. Although absence of long-term data precludes definite conclusions, evidence suggests that porcupine currently are far less common than they were during the twentieth century. Sharp declines in the region are plausible, given the low reproductive capacity of the species. North American porcupines typically have a single litter of one offspring per year after a 210-d gestation period, with females not breeding until they are about 18 months old (Woods 1973, Higgins et al. 2000). Demographic modeling indicates that moderate increases in predation or winter mortality can make populations nonviable (Pokallus and Pauli 2015). Decreases in porcupine populations have been documented in some other regions within the continental species range (Hale and Fuller 1996, Sweitzer et al. 1997, Wall 2007, Horowitz 2015, Appel et al. 2017).

Past and current direct and indirect human-caused mortality and land-use changes certainly may have affected porcupine populations in the region. South Dakota has no season restrictions or bag limits for porcupine harvest by landowners, resident youths, or holders of a Predator/Varmint, Furbearer, or hunting license (South Dakota Game, Fish and Parks 2019). Although porcupines seem to have been common in the Black Hills until the last 2 decades, management to reduce porcupine damage during much of the twentieth century could be a contributing factor in any declines. However, our field surveys included several National Park Service units where direct human-caused mortality, other than roadkill, has been low or absent, and where land-use change is minimal. Moreover, porcupines commonly are observed in many grasslands and woodlands elsewhere in western South Dakota and in adjacent eastern Wyoming and Montana (L. Dombro personal observation). During 12 total days of deer hunting, D. Mergen observed 11 porcupines during 2017–2018 in eastern Jackson County, South Dakota, about 200 km east of the Black Hills. In contrast, during the 2017 and 2018 deer seasons in the Black Hills, Mergen observed no porcupines in 34 d of deer hunting. Keinath et al. (2015) estimated that 9–11 porcupines were present in the 545-ha Devils Tower National Monument, Wyoming, during winter 2014–2015 (Fig. 1). The monument is

TABLE 1. Historical sources that reported information about the nineteenth-century distribution of mammals in the Black Hills of western South Dakota.

Source	Selected Black Hills observations	Notes
Hayden 1862	Recorded Black Hills observations of a marmot, red squirrels, and numerous bird and plant species.	Regarding porcupines, Hayden noted only that the porcupine "occurs rarely throughout Upper Missouri country," referring to the broad region encompassing multiple present-day U.S. states.
Grinnell 1875	Observations of terrestrial rodents are brief, but species collected in the Black Hills include red squirrels, a flying squirrel (presumably *Glaucomys sabrinus*), and a "western woodchuck" (presumably yellow-bellied marmot).	Grinnell documented fauna observed during Custer's 1874 expedition from North Dakota through the Black Hills. The only porcupine observations noted were 2 animals captured in North Dakota far outside the Black Hills.
Dodge 1876	Noted Black Hills observations of beaver, red squirrels, woodchuck [presumably marmot], chipmunks, mice, and numerous bird species.	Dodge documented observations in his role as escort to a scientific expedition to the Black Hills in 1875.
Bailey 1888	Noted the Black Hills occurrence of red squirrels, marmots, chipmunks, and many native nocturnal small rodent species.	Bailey provided abbreviated regional species accounts of mammals of the Dakotas and Minnesota. He described the porcupine as common in cottonwood floodplains in Dawson County, Montana, but made no mention of them with respect to the Black Hills.
Allen 1895	Described species now classified as red squirrels and yellow-bellied marmots as being common in the Black Hills; observations or notes about collections of many other rodent taxa are included as part of a broader coverage of the region's mammalian fauna.	The only porcupine observations mentioned by Allen (1895:265) were with regard to the species being "not uncommon" along the Cheyenne River and in the Badlands, both outside of the Black Hills.

at the northwest edge of the broader Black Hills region, in the disjunct Bear Lodge Mountains.

Rapid near-eradication of porcupine populations by mountain lions (*Puma concolor*) has occurred elsewhere in the western United States (Sweitzer et al. 1997). The putative decline in Black Hills porcupine populations has occurred over a period of rapid increases in mountain lion abundance. Although mountain lions historically were common in the region, bounties were established in 1889, and by the early 1900s the species was nearly extirpated in the Black Hills (Fecske et al. 2003). Due to immigration and reproduction, the population grew rapidly from about 10 lions in 1996 to 251 lions in 2007 (South Dakota Game, Fish and Parks 2010). Porcupines are considered primary prey for mountain lions in the region (Thompson 2009), and dispersing mountain lions in the northern Great Plains commonly show evidence of encounters with porcupines (or porcupine carcasses) (Thompson et al. 2009). The first few years after a mountain lion hunting season was authorized (2005) for the SD Black Hills, every lion that was necropsied by South Dakota Game, Fish, and Parks personnel had evidence of encounters with porcupines (i.e., porcupine quills in the mouth, lips, or paws). More recently, the only lions brought in for necropsy that have showed evidence of porcupine encounters were the ones taken from areas outside the Black Hills (S. Griffin personal communication).

Although these observations suggest that predation may have caused a rapid population decline, factors such as habitat changes, direct human impacts, or disease could have caused or contributed to any decline. Moreover, mirroring questions about California porcupine populations (Appel et al. 2017), we found that the twentieth-century abundance of porcupines in the Black Hills may not be representative of earlier historical conditions. Repeatedly, scientists and naturalists documenting latter-nineteenth-century observations and records of mammals in the northern Great Plains did not report any observations of porcupines in the Black Hills, despite noting observations of other rodents (Table 1). In describing his experiences with wildlife in the

Black Hills from circa 1880 to 1945, Coats (1945:10) noted that "No porcupines were here when I first came. . . . Now they are everywhere in the Hills and doing a lot of damage to our growth pine timber." Such observations suggest that porcupine abundance in the Black Hills increased during the 1900s, potentially due to near-eradication of mountain lions or other factors. Habitat quality may have changed dramatically for porcupine, as twentieth-century fire suppression and logging drove landscape-level increases in pine density (Brown 2006, Freeman 2015).

This study points to a variety of research and monitoring needed to better understand and manage the region's porcupine population, including publicizing the value of documenting any porcupine sightings. Further consideration of the species' management status in the Black Hills may be warranted, but this could be challenging given uncertainty about the pre-twentieth-century abundance of the porcupine and its reputation as a pest species (Roze 2009). Conversely, the porcupine's pest status is partly due to its effects as an arboreal herbivore capable of feeding on tree leaves and inner bark (Woods 1973, Coltrane 2012). Such agents of disturbance and damage can shape forest composition and availability of habitat for other species (Bull et al. 1997, Shepperd and Battaglia 2002, Seager et al. 2013). Relatively few studies have examined ecological impacts of porcupine herbivory beyond direct effects on forage trees, with some consideration of effects on tree species composition and occurrence (Gill and Cordes 1972, Woods and Zeglen 2003, Rivet et al. 2017), forage-species genetics (Linhart et al. 1989, Berteaux et al. 2007), and secondary interaction with, and provisioning of, resources for other species (Shapiro 1949, Ilse and Hellgren 2007). Regardless of its ecological roles, the porcupine has traditional cultural significance to many North American indigenous nations, including those of the Black Hills region (Orchard 1916, Wall 2007, Roze 2009). As a large and nonelusive rodent with unique defensive adaptations, the porcupine offers wildlife-viewing opportunities and is a source of fascination for many nonscientists (e.g., Hiller 1990, Sherman 2018). Throughout the porcupine's range, wildlife managers should be aware that the low reproductive potential of the North American porcupine makes its populations vulnerable to moderate decreases in survival.

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