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Dispersal movements of subadult cougars from the Black Hills: the notions of range expansion and recolonization

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Abstract. Dispersal plays a vital role in cougar (*Puma concolor*) population ecology, creating genetic viability and maintaining gene flow between populations. The naturally recolonized cougar population in the Black Hills is at the edge of the species' range in North America and completely surrounded by the grasslands of the Northern Great Plains. Our objective was to document dispersal movements and possible range expansion of subadult cougars captured within the Black Hills ecosystem of southwestern South Dakota and eastern Wyoming. Twenty-four ($n = 14$ males, $n = 10$ females) subadult cougars were captured in the Black Hills. Independence of cougars from females averaged 13.5 months (range = 10–16 months) from parturition; dispersal occurred 1–3 months post independence. Males dispersed (mean = 274.7 km SE 88.3) farther than females (mean = 48.0 km SE 10.9), with females exhibiting 40% philopatry. We documented several ($n = 6$) long-distance dispersal movements (>250 km) of male cougars and hypothesize that males making long-distance movements were in search of available mates. The long-distance cougar dispersal movements documented by our study indicate that range expansion and habitat recolonization are occurring and further suggest proactive efforts to increase public knowledge of cougar ecology in areas where cougars are recolonizing previously occupied range.

Key words: Black Hills; cougar; dispersal; long-distance dispersal; *Puma concolor*; range expansion; recolonization; South Dakota; Wyoming.

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Introduction

Dispersal is pivotal to population ecology and dynamics of the cougar (*Puma concolor*) in North America. Dispersal has been defined as the permanent movement away from an individual's natal home-range/area (Greenwood 1980). Dispersal is a crucial aspect of population demographics facilitating genetic transfer helpful toward maintaining healthy wildlife populations across large landscape-scale levels (Sinclair et al. 2001, Anderson et al. 2004). Howard (1960) classified dispersal as innate or environmental. Innate dispersal is considered a predisposition to move beyond the confines of a parental home-range, whereas environmental dispersal is in response to "crowded situations" and density dependence (Howard 1960).

Cougar populations across the western United States have shown interrelatedness and movement among populations (Culver et al. 2000, Sweanor et al. 2000, Anderson et al. 2004), Recent genetic analyses classified all cougars ranging north of Argentina as one interrelated subspecies (*P. c. cougaur*; Culver et al. 2000), and it was found that across the Wyoming Basin geographically separate populations were considered panmictic (Anderson et al. 2004). Dispersal among cougar populations allows for genetic material to be introduced and intermixed between otherwise geographically isolated regions (Sweanor et al. 2000, Logan and Sweanor 2001). As habitat fragmentation increases throughout cougar range, movement among populations remains critical to maintain genetic population viability (Beier 1995, Sinclair et al. 2001).

Cougar populations in the western United States increased in the latter portions of the 1900s (Pierce and Bleich 2003). Within the last decade, a noticeable increase in verified cougar presence east of established breeding ranges suggest cougars are recolonizing historic habitat (Cougar Network 2007). As large carnivores extend their current range, increased knowledge of their movements in urban and rural areas is needed to identify conservation and management issues that should be addressed. Our objective was to document dispersal of a semi-isolated cougar population on the eastern edge of known cougar range. We also were interested in documenting and assessing movements of cougars traversing areas that may have been devoid of cougars for >100 years.

The cougar population of the Black Hills of South Dakota and Wyoming provides a prime example of a naturally recolonized, semi-isolated cougar population on the edge of its current distribution (Beier 2010). We consider cougars in the Black Hills semi-isolated in that they are not contiguously connected to western breeding cougar populations, but emigration is likely (Fecske 2003, Anderson et al. 2004). The Black Hills ecosystem is completely surrounded by the Northern Great Plains (Fig. 1), with the closest breeding populations occurring in the Bighorn Mountains of Wyoming (200 km to the west), Laramie Range of Wyoming (160 km to the southwest) and the Badlands of North Dakota (120 km to the north/northeast). Cougars in the Black Hills were nearly if not entirely extirpated from the region by the turn of the 20th Century (Froiland 1990). State protection and management, cessation of poisoning, an increase in prey species, and a lack of competition from other large carnivores allowed the cougar population to rebound to a viable population by the late 1990s. Intensive research was initiated on the Black Hills cougar population in 1998 (Fecske 2003, Thompson 2009), allowing a temporal assessment of the population.

Study Area

The Black Hills are located in west-central South Dakota and northeastern Wyoming, representing the eastern most extension of the Rocky Mountains, and corresponding in age to the oldest mountains in North America (Froiland 1990). Our study area encompassed the Black Hills (Fig. 1), covering approximately 8,400 km^2 (Fecske et al. 2004). The Black Hills are a dome-shaped structure, sloping more steeply to the east than from the west with highest elevation of 2,207 m above mean sea level (Froiland 1990). Soils of the Black Hills are identified as the gray wooded soil region, which is unique to South Dakota (Froiland 1990). The Black Hills ecosystem is comprised of four distinct vegetation complexes: 1) Rocky Mountain coniferous forest, 2) Northern coniferous forest, 3) Grassland complex, and 4) Deciduous complex. Forest cover in the Black Hills is predominantly ponderosa pine (*Pinus ponderosa*) with co-dominants of white spruce (*Picea glauca*) and quaking aspen (*Populus tremuloides*).

Primary prey species available on the study area included: white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*) and porcupine (*Erethizon dorsatum*), along with assorted small mammal species and domestic/livestock species (Higgins et al. 2000). The predator guild of the Black Hills included coyote (*Canis latrans*) and bobcat (*Lynx rufus*); wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and black bears (*Ursus americanus*) were extirpated from the region in the late 1800s to early 1900s (Higgins et al. 2000).

Methods

We captured cougars from 2003–2006 throughout the Black Hills study area primarily with the aid of hounds, as well as opportunistic use of walk-in live traps, foot-hold snares (Logan et al. 1999), and leg-hold traps with offset jaws. We immobilized cougars using a Telazol (2.2 mg/lb) and Xylazine (0.45 mg/lb) mixture (Kreeger 1996) based on estimated live animal body weight. Captured cougars were aged by tooth wear and

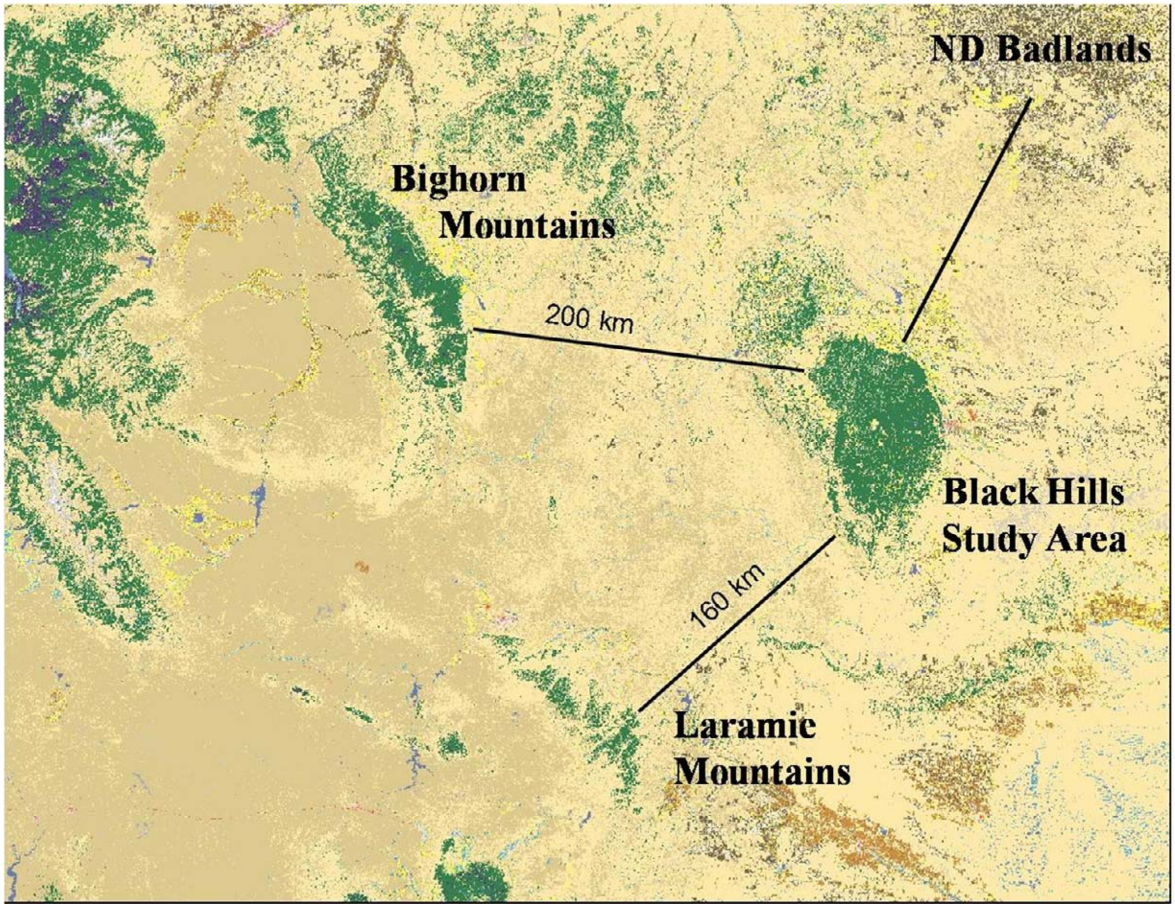

Fig. 1. Map of the Black Hills study area (approximately 8,400 km^2), and proximity to nearest breeding cougar populations.

pelage characteristics (Anderson and Lindzey 2000), and animals >10 months old were fitted with adult VHF radiotransmitters (Telonics, Inc., Mesa, Arizona, USA). Immobilized cougars were reversed (0.125 mg/kg Yohimbine), released on site and observed from a distance to assure safe recovery. We captured kittens (<2 months old) of radio-marked females to determine age of independence and dispersal. Kittens were fitted with expandable VHF radio-collars (Telonics, Inc., Mesa, Arizona, USA). Capture methods followed recommendations of the American Society of Mammalogists and were approved by the Institutional Animal Care and Use Committee (Approval No. 02-A034) at South Dakota State University.

We located study animals weekly via aerial telemetry from a fixed-wing aircraft, along with ground triangulation. Animal locations were plotted in ArcGIS (ESRI, Redlands, California, USA). Dispersal distances (straight line) were calculated from capture point to: site of death, last known location, or home-range center-point if the animal dispersed and successfully established a home-range. We considered a home-range successfully established when an animal resided in an area for >8 months post dispersal. In instances where kittens were captured at dens, we used the natal home-range center-point as the site of capture. We considered cougar kittens independent when they separated from the mother without returning (generally ≥7 sequential days), and backcalculated the last known family unit location to document age of independence. We considered that dispersal occurred once cougar kittens became independent from the mother and siblings and used the date at onset of independent locations for individual initiation of dispersal. Home-ranges were calculated (95% Adaptive Kernel) when necessary using the Home-range Extension in ArcGIS. We chose bandwidths that resulted in the lowest least squares-crossed validation scores (LSCV) to create smoothed home-range polygons (Kie et al. 2002). Cougars that established home-ranges with >5% overlap of natal home-ranges were considered philopatric (Sweanor et al. 2000). If an animal established a home-range within the study area, we considered it successfully recruited into the Black Hills cougar population.

Results

We captured 14 subadult male and 10 subadult female cougars in the Black Hills 2003–2006. We also captured and marked 18 kittens from seven separate litters. Age of independence averaged 13.5 months (range = 10–16 months) with dispersal occurring 1–3 months after animals became independent from mothers. Upon reaching independence, subadult cougars of the same sex generally traveled together for a short time before separating and dispersing solitarily. Based on data from four same-sex sibling groups, independent littermates commingled for an average of 70.8 days (range = 65–83 days). Three female siblings traveled together for 83 days before disbanding. Three separate male sibling groups traveled together for 65 ($n = 2$ siblings), 66 ($n = 3$ siblings), and 69 ($n = 3$ siblings) days, respectively, after becoming independent from the birth female. We noticed no difference in age of independence or age of dispersal between sexes, but the sex ratio of kittens was highly skewed to males (5:1).

Dispersal of 10 subadult female cougars averaged 48.0 km SE 10.9 (range = 12.3–98.6 km). Four (40%) female cougars were philopatric. Several females ($n = 3$) left the study area and established home-ranges or perished. Dispersal of 14 subadult male cougars averaged 274.7 km SE 88.3 (13.3–1,067.0 km). No subadult male cougars were recruited into the cougar population in the Black Hills. All males successfully dispersed from natal areas, but several animals ($n = 6$) died while dispersing before establishing residency. If cougars that died while dispersing were censored, average dispersal distance increased to 450 km SE 123. We documented the longest dispersal movement by a cougar (1,067 km) from the Black Hills to Oklahoma in 2003 (Thompson and Jenks 2005), and 5 other radio-marked cougars moved in excess of 250 km (Fig. 2).

Five subadult female cougars dispersed >50 km from natal ranges, and female cougar dispersal followed a general pattern of moving toward the periphery of the Black Hills (Fig. 3). Male cougars made similar movements to the periphery, following the edge of the forested regions of the ecosystem before leaving the Black Hills to traverse prairie and agricultural habitats.

Discussion

The process of dispersal is important to maintain genetic transfer among cougar populations via immigration or emigration (Sweanor et al. 2000, Anderson et al. 2004, Culver et al. 2000), and to reduce strife among competitive individuals (Logan and Sweanor 2001, Maehr et al. 2002). As seen in other cougar populations, subadult male cougars in the Black Hills dispersed farther than females. Although dispersal rates of our female cougars were comparable to those documented by Sweanor et al. (2000), both male and female cougars dispersed greater distances, on average, than documented in previous research throughout cougar range in North America (Hemker et al. 1984, Logan et al. 1986, Beier 1995, Spreadbury et al. 1996, Sweanor et al. 2000, Logan and Sweanor 2001). Male and female Florida panthers dispersed on average 68.4 km and 20.3 km, respectively with a maximum dispersal of 224.1 km for a subadult male (Maehr et al. 2002). Prior to our results in the Black Hills, the maximum straight-line dispersal distance of a cougar was that of a subadult male dispersing 483 km from the Bighorn Mountains of Wyoming to Colorado (Thompson and Jenks 2005). The maximum documented female cougar dispersal movement occurred in the basin and range landscape of north-central Utah, where a female dispersed 357 linear km, while covering an actual distance of 1,341 km (Stoner et al. 2007).

Age of independence and dispersal was typical for cougars in western North America (Beier

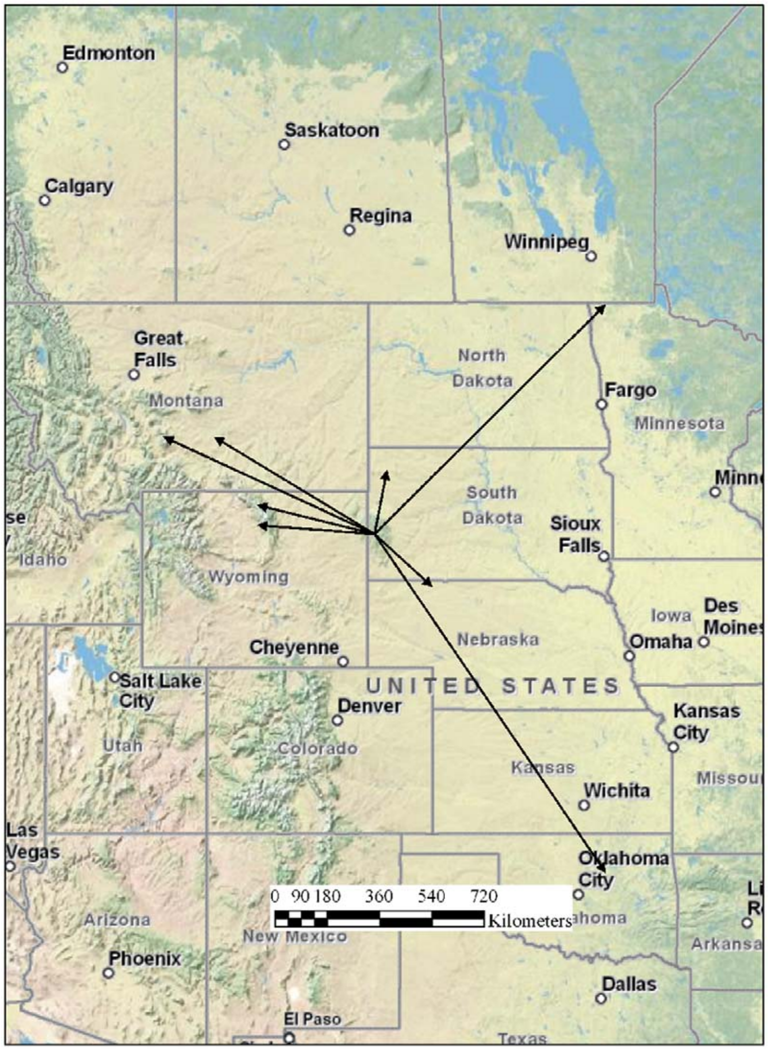

Fig. 2. Examples of dispersal movements (straight-line) by subadult male cougars from the Black Hills of South Dakota, 2003–2006.

1995, Sweanor et al. 2000, Logan and Sweanor 2001, Pierce and Bleich 2003). We noted that upon reaching independence same sex littermates commingled for 2–3 months before disbanding and making solitary dispersal movements. Although documented (Quigley and Hornocker 2010), there is a lack of published material related to this subadult commingling behavior in cougars, and it would be of interest to document the gregarious activities of an otherwise solitary carnivore, especially as it relates to hunting behavior and prey sharing. Ancillary tracking data suggested siblings did share consumption of prey, however, we do not know if cooperative hunting efforts occurred during this short phase of cougar life history.

We documented longer multiple long-distance movements from male and female cougars than previously found, with many of these animals leaving the Black Hills and crossing regions considered unsuitable for occupation by cougars. Dispersing animals therefore have the ability to immigrate to regions within cougar range that may have otherwise been considered geographically separated. It has been suggested that habitat barriers may limit movements of cougars among populations (McRae et al. 2005) and while this may be evident in areas with higher

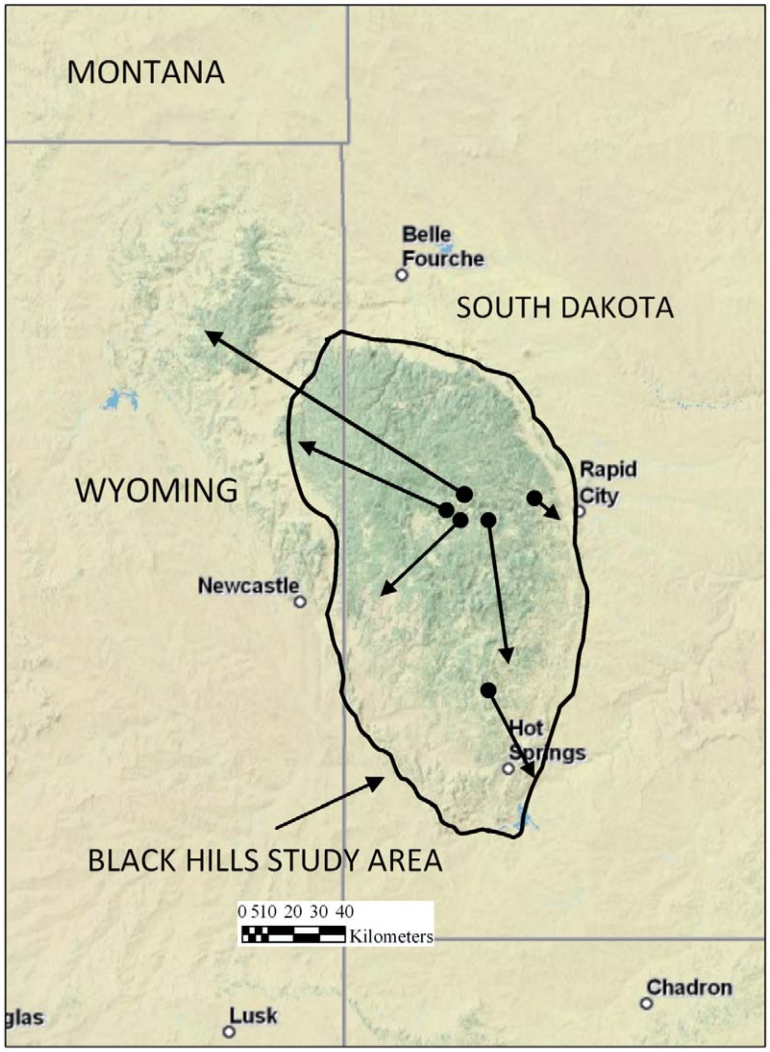

Fig. 3. Dispersal movements by subadult female cougars to peripheral regions of the Black Hills study area, 2003–2006.

human habitation, the rural yet heavily fragmented agricultural landscapes crossed by cougars emanating from the Black Hills suggest these types of habitat constraints are not preventing cougar dispersal movements. Sweanor et al. 2000 documented that cougars moved quickly between habitat patches, as has been documented with snow leopards (*Uncia uncia*) traversing atypical leopard habitat (McCarthy 2000). Previous modeling exercises suggested cougars use riparian drainages while dispersing into regions of the Midwest as well as the potential of using grassland habitats (Larue and Nielsen 2008).

During the course of our study, we relied solely on VHF technology and aerial locations to document dispersal, which somewhat hampered the ability to finitely assess habitat use and rate of departure of dispersing cougars once marked individuals dispersed >50 km from the study area. One individual (M31) was documented using a riparian corridor to disperse from the study area, with subsequent large movements to patches of suitable lion habitat (Fig. 4). The location gathered on 16 September 2010 represented a 93 km movement to patch of suitable lion habitat (approximately 632 km^2) in ≤14 days. Cougar M31 dispersed from this region in <5 days based on aerial telemetry. Further

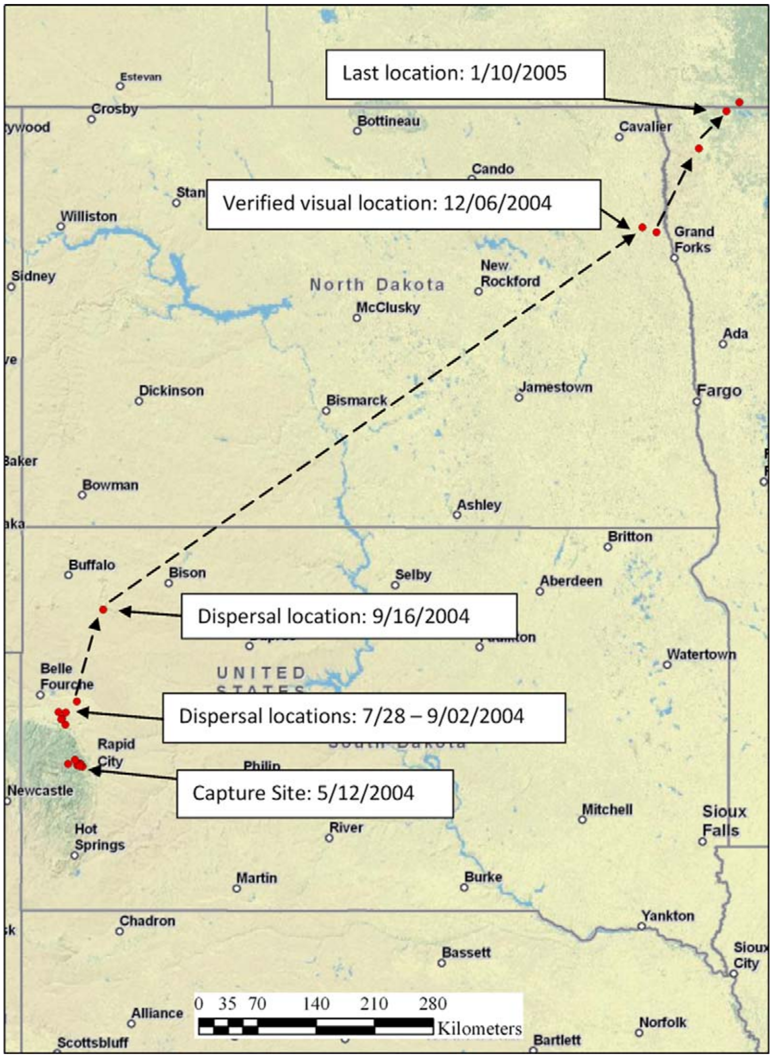

Fig. 4. Dispersal movements by subadult male cougar M31. Data includes capture site, dispersal movements from the study area implementing a riparian corridor, and subsequent long range dispersal movements.

movements gathered in North Dakota and Minnesota were the result of a verified sighting by the public and subsequent aerial locations conducted by North Dakota Department of Fish and Game and Minnesota Department of Natural Resources. To better document fine-scale attributes of long-distance dispersal movements, it would be advantageous to implement global positioning system (GPS) technology on marked individuals to allow for a more in-depth assessment of travel rates of dispersing cougars along with identification and quantification of travel corridors across atypical habitat.

Female cougars elsewhere are generally philopatric (Logan and Sweanor 2001, Pierce and Bleich 2003), but that was not the case in the Black Hills. Movements of females were indicative of resource and intraspecific competition (e.g., environmental dispersal; Howard 1960); rather than establishing a home-range overlapping or adjacent to natal ranges, several females moved either out of the Black Hills or to the outermost edge of available forested habitat within the study area to establish a successful home-range. During our study, females in the Black Hills may have had decreased philopatry compared with other populations due to increased competition between mothers and female offspring as well as using dispersal as a mechanism to reduce inbreeding (Logan and Sweanor 2001). Although inbreeding avoidance has been suggested as a causal factor for male dispersal, it also may facilitate female dispersal in fully occupied habitats. Biek et al. (2006) found that intrapopulation female movements were beneficial for maintaining population genetic viability.

"Obligate dispersal" has been postulated as a behavior adopted by subadult male cougars to discourage inbreeding, regardless of population density (Logan and Sweanor 2001). Subadult male cougars in the Black Hills dispersing from one end of the study area to the other (>100 km) would generally negate instances of inbreeding based on home-range size and social makeup of resident females; however, we failed to document a successful dispersal movement of a male remaining on the study area. While prey species are generally abundant throughout the region, resident males are generally not conducive to allowing new individuals to establish home-ranges within their defended home-range (Logan and Sweanor 2001, Maehr et al. 2002). Competition for mates and resources seems to drive dispersal of subadult male and some female cougars out of the study area into less preferred habitats. More importantly dispersal movements of cougars in the Black Hills may be a function of combined effects of both innate and environmental dispersal (Howard 1960) for both male and female cougars.

Driving factors of dispersal (i.e., inbreeding avoidance, lack of resources/density dependence) would not account for subadult male cougars traveling >300 km from the Black Hills. After a cougar left the study area, it was traversing areas devoid of breeding cougar populations for at least 100 years, effectively eliminating potential intraspecific competition. Competition for naïve prey (Berger et al. 2001) would be minimal. Unless an animal was successful in reaching regions to the west where bears and wolves occur, the largest source of interspecific competition would come from coyotes and humans. Historically, cougars were noted in riparian regions of North and South Dakota and the Dakota Badlands (Roosevelt 1998, Young and Goldman 1946). Hornocker (Cougar Network 2007) noted an abundance of cougar habitat in the Midwest, and recently North Dakota modeled and mapped 2,706 km^2 of high quality cougar habitat approximately 180 km from the study area (North Dakota Game and Fish Department [NDGFD] 2007); suggesting habitat availability is not a limiting factor outside of the Black Hills. We suggest the driving force for these long-distance dispersals is in fact related to breeding activity and creating genetic progeny—*mate procurement hypothesis*. When subadult male cougars cross regions void of extant populations, they continue to travel until a breeding population is encountered and where they are able to establish residency. Data from marked individuals showed that dispersing animals were successful in locating areas with prey and adequate habitat (Thompson et al. 2009), however unless dispersing into areas with extant breeding cougar populations, subadult males continued to disperse. For example, a long-distance movement by a subadult male cougar through western South Dakota, North Dakota and Minnesota traversed regions with ample prey and habitat (Fig. 4); however, the area lacked established female cougars (NDGFD 2007). Three long-distance dispersers (M17, M19, and M51) successfully reached breeding cougar populations in Montana (M17 and M19) and Wyoming (M51) and upon finding available unoccupied habitat, established home-ranges therein. All three animals were harvested after remaining within their respective home-ranges for at least one year. Other radio-collared cougars dispersing >200 km were not known to establish home-ranges, possibly because they were unable to locate breeding populations with vacant home ranges. Based on our results, importance of finding an available mate may supercede the effects of habitat and prey availability (Hornocker 2010) as they relate to cougar dispersal. This notion may apply to other large North American carnivores (i.e., bear spp., jaguars [*Panthera onca*] and wolves) capable of making long-range movements to facilitate recolonization of extirpated populations.

Management/Conservation Implications

Range expansion is a new phenomena occurring for several large carnivores throughout North America (cougars [Pierce and Bleich

2003]; grizzly bears [Pyare et al. 2004]; and wolves [U.S. Fish and Wildlife Service 2009]). Dispersal of cougars originating in the Black Hills provide evidence that recolonization of cougars is occurring and is further substantiated by increased verified cougar sightings throughout midwestern, southern, and eastern North America (Cougar Network 2007, Beier 2010). For example, North Dakota recently documented their first breeding cougar population in the western badlands region of the state since the 1800s (NDGFD 2007). Although subadult male cougars make most recolonizing movements, female cougars also have dispersed into former cougar ranges. Dispersal of female cougars, especially in a population on the edge of cougar range, constitutes true range expansion and recolonization of the species to former habitats.

With long-range dispersal and recolonization movements in mind, it is essential for wildlife agencies in former cougar ranges throughout North America to be proactive in their dealings with cougar conservation and with constituents residing in former unoccupied habitats where cougars may be dispersing. Pre-emptive management plans, bolstered with public education on cougar ecology and the reappearance of a top-level carnivore, are essential to minimize conflicts that occur between cougars and humans as cougars attempt to recolonize former areas (Beier 2010). Range expansion and colonization of cougars are highly contentious topics among the public. We suggest anticipatory management/conservation efforts and public education to help avoid future conflicts between transient recolonizing cougars and resident humans. Managing agencies must remain transparent in efforts with the public to maintain credibility when dealing with the resurgence of large carnivores.

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