

ECOLOGY OF MOUNTAIN LIONS (*Puma concolor*) IN THE NORTH DAKOTA
BADLANDS: POPULATION DYNAMICS AND PREY USE

BY

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A thesis submitted in partial fulfillment of the requirements for the

Master of Science

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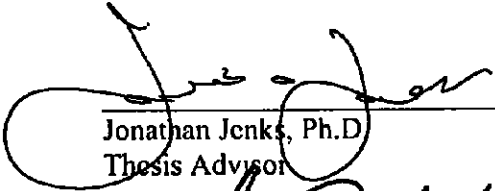
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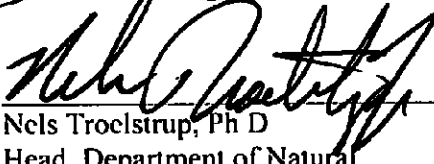
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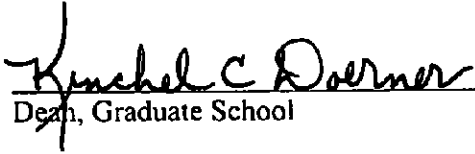
2014

ECOLOGY OF MOUNTAIN LIONS (*Puma concolor*) IN THE NORTH DAKOTA
BADLANDS. POPULATION DYNAMICS AND PREY USE

This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science in Wildlife and Fisheries Sciences degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidates are necessarily the conclusions of the major department.


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ABSTRACT

ECOLOGY OF MOUNTAIN LIONS (*Puma concolor*) IN THE NORTH DAKOTA
BADLANDS: POPULATION DYNAMICS AND PREY USE

DAVID WILCKENS

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Mountain lions (*Puma concolor*) have recently recolonized the North Dakota Badlands nearly a century after their extirpation; due to the relatively recent reappearance of mountain lions in the region, most population metrics are unknown. From 2011–2013, we fitted 14 mountain lions with GPS collars and ear-tagged an additional 8 to study the characteristics of this mountain lion population and the potential impacts of mountain lion predation on prey populations in the region. Annual adult home ranges averaged $231.1 \text{ km}^2 \pm 21.8$ [SE] for males and $109.8 \text{ km}^2 \pm 20.2$ for females; we did not see seasonal shifts in home range size or distribution for either sex. Home range overlap between adult males averaged $13.7\% \pm 2.4$ [SE]. Average male dispersal within the region was $45.13 \text{ km} \pm 11.7$ [SE]; however, we also documented 2 long-range dispersers (375.87 km and 378.20 km) immigrating into North Dakota from Montana. Estimated annual survival was $42.1\% \pm 13.5$ [SE]. All documented mortalities ($n = 12$) of marked mountain lions were human-caused; hunter harvest ($n = 7$) was the highest cause of mortality. Deer (*Odocoileus* spp.) were the most prevalent item (76.9%) in mountain lion diets. Ungulate kill rates were $1.09 \text{ ungulates/week} \pm 0.13$ [SE] in summer and $0.90 \text{ ungulates/week} \pm 0.11$ in winter. Estimates of total biomass consumed were $5.8 \text{ kg/day} \pm 0.56$ [SE] in summer and $7.2 \text{ kg/day} \pm 1.01$ in winter. Scavenge rates were 3.7% in

summer and 11.9% in winter. Prey composition included higher proportions of nonungulates in summer (female = 21.54%; male = 24.80%) than in winter (female = 4.76%; male = 7.46%). Proportion of juvenile ungulates in mountain lion diets increased following the ungulate birth pulse in June (June–August = $60.67\% \pm 0.09$ [SE]; September–May = $37.21\% \pm 0.03$), resulting in an ungulate kill rate 1.61 times higher during the fawning season (1.41 ungulates/week ± 0.15) than during the remainder of the year (0.88 ungulates/week ± 0.13). Our study provides region-specific population characteristics of a newly recolonized and previously unstudied mountain lion population within the Little Missouri Badlands of North Dakota.

CHAPTER 1: GENERAL INTRODUCTION

Mountain lions (*Puma concolor*) historically have had the widest geographic distribution of all terrestrial mammals (excluding humans) in the Western Hemisphere, ranging from Canada to Patagonia (Logan and Sweanor 2001; Laundré and Hernández 2009). Mountain lions are a highly adaptable species, inhabiting diverse environments from deserts (Logan and Sweanor 2001) to rainforests (Laundré and Hernández 2009) to boreal forests (Knopff et al. 2010). In North America, mountain lions were found across the continent prior to the arrival of Europeans; however, colonization by Europeans initiated an era of hostility towards predators in North America and a trend of habitat loss from development and agriculture, leading to declines in prey populations (Gill 2009). Predators were targeted and killed by settlers to eliminate perceived risks to themselves and livestock (Gill 2009); this persecution led to near eradication of mountain lions in the eastern United States (except Florida) and contraction of mountain lion distribution to approximately one half of their previous range in North America (Hornocker and Negri 2009). Animosity towards mountain lions continued into the early 1900s when many states promoted the bounty system, and the federal government employed hunters and trappers in an effort to reduce/eliminate mountain lion populations (Gill 2009); although, North Dakota never had a bounty system on mountain lions (McKenna et al. 2004). Since 1965, regulations protecting mountain lions from extreme harvests (e.g., eliminating bounty systems, regulated harvest seasons) have been implemented across most Western states (excluding Texas), offering some type of protection for mountain lion populations (Logan and Sweanor 2001). These regulations have allowed mountain

lion populations to rebound. Recently, mountain lions have expanded their range eastward, recolonizing areas in the Midwest (e.g., Black Hills of South Dakota, western Nebraska, Badlands of North Dakota) where they were previously extirpated (LaRue et al. 2012). Research on these newly reestablished Midwestern populations has been limited to the Black Hills of South Dakota (e.g., Fecske 2003, Thompson 2009, Jansen 2011).

Historically, mountain lions were found across all of North Dakota; however, they were considered rare outside of the western portion of the state (Bailey 1926). Mountain lions were believed to be extirpated from North Dakota in the early 1900s (Bailey 1926), but have recently recolonized the Badlands region of the state beginning in the early 2000s (North Dakota Game and Fish Department 2006). Currently, a relatively small breeding population of mountain lions inhabit the Little Missouri Badlands in western North Dakota and is managed using a regulated, limited harvest season (Tucker 2013). This population persists at the eastern extent of mountain lion range (excluding Florida; LaRue et al. 2012) and is separated from other breeding populations by expanses of Northern Great Plains grasslands; although, immigration into North Dakota has been previously documented from the neighboring mountain lion population in Black Hills, South Dakota (Thompson and Jenks 2010).

As a result of this recent reappearance of the species, no previous mountain lion research has been conducted in the region and thus, many characteristics of the population are unknown. From 2011–2013, we studied mountain lions occupying the North Dakota Badlands (Figure 1) to document baseline population characteristics. Our objectives were to 1) estimate annual home range size of adult mountain lions, 2)

compare the effects of season and sex on home range size, 2) calculate overlap of adult male home ranges, 4) determine dispersal characteristics (e.g., age at dispersal, dispersal distance) of subadults, 5) estimate survival rates, and 6) quantify cause-specific mortality. Additionally, mountain lions represent the lone apex predator in the Badlands. This has led to questions on their potential impacts on prey populations. Thus, we studied mountain lion food habits within the region to answer the following 5 research questions: 1) what is the prey composition of mountain lion diets, 2) how many ungulates do mountain lions kill, 3) what effect does scavenging have on ungulate consumption rates, 4) what effect does season have on mountain lion feeding habits, and 5) what effect does demographic status have on mountain lion feeding habits?

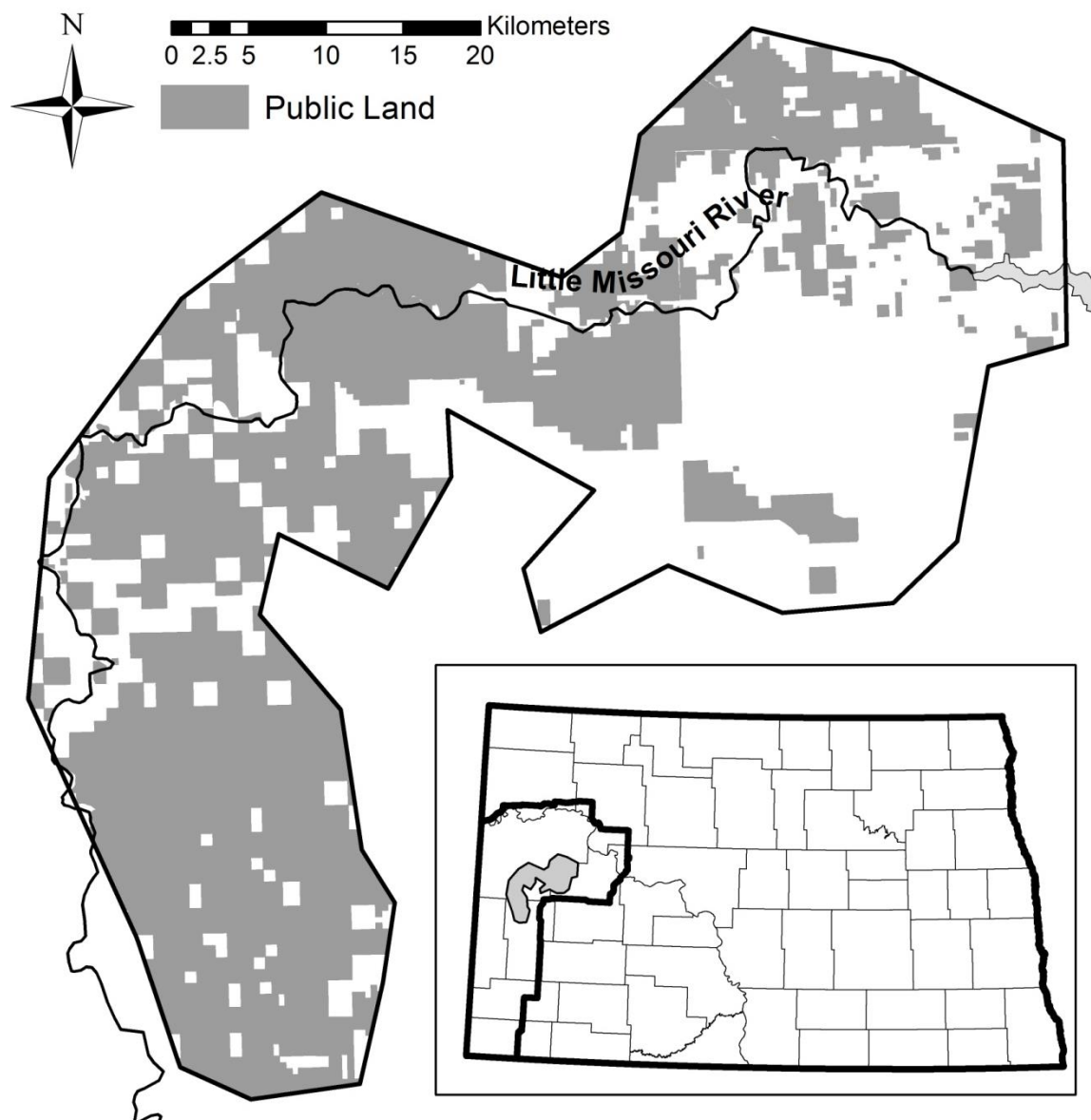
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FIGURE 1.—Our study area was focused within the Little Missouri Badlands of western North Dakota from 2011–2013.



**CHAPTER 2: POPULATION CHARACTERISTICS OF MOUNTAIN
LIONS (*Puma concolor*) IN THE NORTH DAKOTA BADLANDS**

*This chapter was prepared for submission to the American Midland Naturalist and was
coauthored by Stephanie A. Tucker, Daniel J. Thompson, and Jonathan A. Jenks.*

Population Characteristics of Mountain Lions (*Puma concolor*) in the North Dakota

Badlands

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ABSTRACT.—Mountain lions (*Puma concolor*) have recently recolonized the North Dakota Badlands nearly a century after their extirpation; due to the relatively recent reappearance of mountain lions in the region, most population metrics are unknown. We studied the characteristics of this mountain lion population from 2011–2013. Annual home ranges averaged $231.1 \text{ km}^2 \pm 21.8$ [SE] for males and $109.8 \text{ km}^2 \pm 20.2$ for females; we did not observe seasonal shifts in home range size or distribution for either sex. Home range overlap between adult males averaged $13.7\% \pm 2.4$ [SE]. Average male dispersal distance within the region was $45.13 \text{ km} \pm 11.7$ [SE]; however, we also documented 2 long-range dispersers (375.87 km and 378.20 km)

immigrating into North Dakota from Montana. Overall estimated annual survival was $42.1\% \pm 13.5$ [SE]. All documented mortalities ($n = 12$) of marked mountain lions were human-caused; hunter harvest ($n = 7$) was the highest cause of mortality, followed by illegal harvest ($n = 2$), depredation removal ($n = 2$), and vehicle collision ($n = 1$). Our study provides region-specific population characteristics of a newly recolonized and previously unstudied mountain lion population within the Little Missouri Badlands of North Dakota.

INTRODUCTION

Documenting movement patterns (*e.g.*, home range, dispersal) of mountain lions (*Puma concolor*) is essential for understanding their interactions with the environment in which they inhabit, as well as with one another. A home range is commonly described as an area regularly utilized by an individual to gather food, mate, and/or care for young; brief excursions outside of this general use area are typically not included in home range estimates (Burt, 1943). Individuals, however, may show seasonal shifts in home range characteristics. Seasonal shifts in mountain lion home range size and distribution have been linked to the seasonal habits of prey items, particularly ungulates, within the same region. Studies conducted in regions with migratory ungulate prey have documented seasonal variation in mountain lion home ranges as they followed prey migrations (Seidensticker *et al.*, 1973; Pierce *et al.*, 1999; Grigione *et al.*, 2002) or contractions/expansions of prey distribution during dry/wet seasons (Dickson and Beier, 2002); these movements are in contrast to studies performed in areas with nonmigratory prey (Sweaner, 1990; Ross and Jalkotzy, 1992; Grigione *et al.*, 2002). Additionally,

mountain lion home ranges are known to vary by sex; male home ranges typically overlap 3 to 5 resident females (Logan and Sweanor, 2001).

Variation in previously reported adult mountain lion home ranges is likely due to a combination of varying ecological conditions (*e.g.*, habitat, prey availability/distribution, mountain lion density) between study areas and differing methods of calculation. Early methods of calculating home range area, including minimum convex polygon (MCP), provide rough estimates of species distributions and habitat use across landscapes; though MCP methodology likely overestimates areas of normal use (White and Garrott, 1990; Kie *et al.*, 2010). However, since the advent of global positioning system (GPS) collar technology, new home range analytical methods such as the Brownian bridge movement model (BBMM; Bullard, 1999) have been developed to maximize use of larger datasets and increased accuracy in location collection, allowing for more precise estimates of both home range size and spatial use patterns (Kie *et al.*, 2010). BBMM, unlike kernel estimates, takes into account the serial correlation of GPS locations and provides a model of landscape movements using Brownian motion to estimate paths traveled between successive GPS locations while determining the probability of an individual being in an area based upon its starting and ending locations (Horne *et al.*, 2007). Estimation of movement paths allows the BBMM to identify travel ways used by individuals and withhold areas of avoidance from home range estimates (Horne *et al.*, 2007). These characteristics of the BBMM provide enhanced understanding of animal movements and habitat use across the landscape. Mapping of adult mountain lion home ranges allows researchers to evaluate distribution

of the population across the landscape, and lends itself to calculating home range overlap (Logan and Sweanor, 2001).

Dispersal has been described as when a subadult leaves its natal home range and does not return (Logan and Sweanor, 2001). Mountain lion dispersal movements are vital to maintenance of genetic diversity and can additionally influence the population dynamics within a region through immigration/emigration (Sweanor *et al.*, 2000). Dispersal characteristics, such as age of dispersal and distance of dispersal, also have the potential to affect survival of dispersing individuals due to inexperience and increased exposure to mortality factors (*e.g.*, hunters, depredation events, road crossings, intraspecific strife; Logan and Sweanor 2001).

Quantifying survival rates is vital to comprehending population dynamics, and researchers must be able to recognize specific causes of mortality events to fully comprehend survival rates. Some natural-caused (*e.g.*, infanticide, intraspecific strife, starvation, disease) and human-caused (*e.g.*, illegal harvest, roadkill) mortalities may not be readily documented in unstudied populations, while other causes of mortality may be well known (*e.g.*, hunter harvest, depredation removal). It is important to consider that these sources of mortality also may have varying impacts on overall survival rates, and thus, population dynamics.

Mountain lions were believed to be extirpated from North Dakota in the early 1900s (Bailey, 1926), but have recently recolonized portions of the state beginning in the early 2000s (North Dakota Game and Fish Department, 2006). Currently, a relatively small breeding population of mountain lions inhabits the Little Missouri Badlands region in western North Dakota (Tucker, 2013). This population persists at the eastern extent of

mountain lion range (excluding Florida; LaRue *et al.*, 2012) and is separated from other breeding populations by expanses of Northern Great Plains grasslands; although immigration into the state has been documented (Thompson and Jenks, 2010). As a result of this recent reappearance, no previous mountain lion research has been conducted in the region and many characteristics of the population are unknown. We studied the mountain lion population occupying the North Dakota Badlands region to document baseline characteristics of this population. The objectives of our study were to: estimate annual home range size of adult mountain lions, compare the effects of season and sex on home range size, calculate overlap of adult male home ranges, determine dispersal characteristics (*e.g.*, age at dispersal, dispersal distance) of subadults, estimate survival rates, and quantify cause-specific mortality.

METHODS

STUDY AREA

We studied mountain lions in western North Dakota, USA, within Billings, Dunn, and McKenzie counties. Our 2,050 km² study area comprised approximately one third of the Little Missouri Badlands Region, and was contained within “Zone 1” of the mountain lion management area, as defined by the North Dakota Game and Fish Department (Tucker, 2013; Figure 1). The Badlands Region is characterized by highly eroded, steep clay canyons and buttes, distributed along the Little Missouri River and ranging in elevation from approximately 570 m to 710 m above mean sea level (Hagen *et al.*, 2005). Vegetation occurring in draws of the northern and eastern slopes was predominately Rocky Mountain juniper (*Juniperus scopulorum*) and green ash (*Fraxinus pennsylvanica*); while riparian areas contained cottonwood (*Populus deltoides*) stands.

Southern and western slopes, plateaus, and bottomlands were often barren or contained short-grass prairie (Hagen *et al.*, 2005). Grass species within the region included blue grama (*Bouteloua gracilis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), Indian ricegrass (*Achnatherum hymenoides*), western wheatgrass (*Pascopyrum smithii*), and little bluestem (*Schizachyrium scoparium*; Hagen *et al.*, 2005). The Killdeer Mountains Region also was located within the study area, and represented a 60 km² island of elevated habitat connected to the Badlands Region by a few small drainages. This area rises 300 m above the surrounding prairie to 1,010 m and is comprised of a mosaic of open grassland and deciduous species, including green ash, quaking aspen (*Populus tremuloides*), burr oak (*Quercus macrocarpa*), paper birch (*Betula papyrifera*), western black birch (*B. niger*), and American elm (*Ulmus americana*), with a dense undergrowth of beaked hazelnut (*Corylus cornuta*; Hagen *et al.*, 2005).

North Dakota's climate is continental; a relatively dry climate (42.7 cm mean annual precipitation) characterized by hot summers (record high 49 C) and cold winters (record low -51 C; Seabloom, 2011). Cattle grazing was the most common land use in the Badlands (Hagen *et al.*, 2005); however, oil and gas development was rapidly increasing within the region and well sites were abundant throughout our study area. Our study area was a mosaic of public (49%) and private land (51%), with the western portion predominately public and the eastern portion predominately private (Figure 1). Public lands within the study area included Theodore Roosevelt National Park (TRNP), the Little Missouri National Grasslands, Bureau of Land Management properties, North Dakota State Trust lands, and the North Dakota Game and Fish Department Killdeer Wildlife Management Area.

Potential ungulate prey for mountain lions included mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*), and pronghorn (*Antilocapra americana*); bison (*Bison bison*) were potential prey within TRNP. Potential nonungulate prey included beaver (*Castor canadensis*), porcupine (*Erethizon dorsatum*), turkey (*Meleagris gallopavo*), and raccoon (*Procyon lotor*). Domestic livestock (*e.g.*, cattle, horses, goats) also were available as prey. Other carnivores including coyote (*Canis latrans*), bobcat (*Lynx rufus*), and red fox (*Vulpes vulpes*), were present as both potential competitors of and prey items for mountain lions.

Mountain lions were classified as a furbearer species in North Dakota, with two regulated harvest seasons; North Dakota's mountain lion hunting season was structured such that the use of hounds is prohibited during the early hunting season, but was permitted in the late hunting season (Tucker, 2013). Hunters pursuing mountain lions without the use of hounds during the early hunting season were likely to follow mountain lion tracks (given proper tracking conditions), use predator calls to attract them into shooting range, or shoot them at chance encounters while in the field hunting other game (*e.g.*, deer, elk). Although hunting without hounds is allowed in the late hunting season, the majority of mountain lions taken during this period were hunted with the aid of hounds (Tucker, 2013).

CAPTURE AND MONITORING

From 2011–2013 we captured mountain lions from established bait (*e.g.*, road-killed ungulates) sites with the use of foot-hold traps and foot-hold snares (Logan *et al.*, 1999). We immobilized mountain lions with a mixture of tiletamine and zolazepam (Telazol; 5.0 mg/kg) and xylazine (Anased; 1.0 mg/kg; Kreeger and Arnemo, 2007),

based on estimated live animal body weight, via dart rifle (Dan-Inject, Børkop, Denmark, EU). We weighed, measured, determined sex, and estimated age (using tooth wear and pelage characteristics [Anderson and Lindzey, 2000]) of captured mountain lions. We classified mountain lions as kittens (dependent on mother), subadults (dispersal until 2.5–3 yrs), or adults (>3 yrs) and fitted mountain lions with real-time GPS radio-collars (Advanced Telemetry Systems [ATS] G2110E, Isanti, Minnesota, USA). We programmed GPS collars to collect 8 locations/day (0000, 0300, 0600, 0900, 1200, 1500, 1800, and 2100 hrs). Collars were set to attempt a GPS fix for 120 seconds at each scheduled fix time (ATS “forest” setting), then transmit those coordinates via satellite every 24 hrs to an automated email system. Collars were programmed with an 10 hour mortality signal. Individuals that were too small to radio-collar were fitted with ear-tags. Upon completion of handling, we administered yohimbine (Yobine; 0.125 mg/kg) to reverse xylazine, released mountain lions on site, and monitored them from a distance to ensure safe recovery (Kreeger and Arnemo, 2007). We captured kittens from collared females by hand at natal den sites at approximately 1 month of age. We weighed, determined sex, and ear-tagged each kitten before returning it to the den site where it was captured. All procedures were approved by the South Dakota State University Animal Care and Use Committee (Approval number 11–080A) and followed recommendations of the American Society of Mammalogists (Sikes and Gannon, 2011).

HOME RANGE ANALYSIS

We estimated annual and seasonal (summer = May 15–November 14, winter = November 15–May 14) home ranges for resident adult mountain lions fitted with GPS collars and with ≥ 10 weeks of locations within a given season. We considered subadults

as residents after 4 months of predictive habits (Ross and Jalkotzy, 1992). For individuals monitored through multiple years or seasons (*e.g.*, multiple winters), we calculated separate home ranges for each year/season. We calculated 95% and 50% home ranges using a BBMM in package ‘BBMM’ (Nielson *et al.*, 2013) in Program R (R Core Team, 2013). We used a maximum time-lag of 185 minutes to exclude non-consecutive locations from Brownian bridge construction and a cell size of 100m. For comparison with previous studies (*e.g.*, Seidensticker *et al.*, 1973; Ross and Jalkotzy, 1992), we also calculated minimum convex polygon (MCP) home ranges using package ‘adehabitatHR’ (Calenge, 2006) in Program R (R Core Team, 2013). We used paired t-tests to compare the BBMM and MCP methods, and analysis of variance tests to compare home ranges by sex and season. We performed these analyses using SYSTAT 11.0 (Systat Software Inc., Chicago, Illinois, USA).

We calculated spatial home range overlap in ArcMap 10 (Environmental Systems Research Institute, Inc., Redlands, California, USA) for adjacent adult males that were radio-collared during the same time period using 95% BBMM home ranges created specifically during the time of concurrent monitoring. We did not capture any adjacent adult females with concurrent monitoring periods and therefore, we did not calculate home range overlap for this demographic group.

DISPERSAL MOVEMENTS

We recorded dispersal distances for subadults by calculating the straight-line distance between initial capture location and either mortality location, last known location (*e.g.*, collar failure), or home range centroid if the animal successfully established a home range after dispersal (Thompson and Jenks, 2010). Additionally, we

calculated average distance between females and their young fitted with GPS collars to estimate age of independence and age of dispersal of young.

SURVIVAL ANALYSIS

We used a known fate model with the logit-link function in Program MARK (White and Burnham, 1999) to estimate monthly and annual survival of radio-collared mountain lions. We included all radio-collared individuals in our survival analysis, including kittens; our youngest collared kittens (~10 mo) were legally harvestable (no visible spots) in North Dakota (Tucker, 2013). We created a monthly encounter history for each individual beginning at capture date and continuing through the end of the year, mortality, or collar failure, for each year it was monitored. Collar failures were right censored; individuals were reentered into the analysis if they were recaptured. We developed a series of *a priori* models using year and time of year (*i.e.*, non-hunting season, early hunting season, late [hound] hunting season) as covariates. We were notified of mortality signals from GPS collars via satellite as soon as collars switched to mortality status; we investigated all mortality signals as soon as possible to collect data on cause-specific mortality.

RESULTS

From 2011–2013, we captured and collared 14 mountain lions including 5 adult males, 2 subadult males, 4 adult females, 1 subadult female, and 2 female kittens (~10 mo); 1 subadult male transitioned to an adult, and the 2 female kittens transitioned to subadults during the study. We also ear-tagged 1 older male kitten (~10 mo), which transitioned to a subadult during the study (via field sightings, and harvest) and 7 (6M, 1F; [~1 mo]) kittens from 2 collared females at natal den sites. In addition to animals

captured in North Dakota, 2 subadult males previously captured and marked in Montana (Charles M. Russell National Wildlife Refuge [CMRNWR]; R. Matchett, CMRNWR, pers. comm.) also were located within our study area; these individuals were included in our analyses of dispersal, survival [MT-M6 only], and cause-specific mortality.

HOME RANGE ANALYSIS

We calculated annual and seasonal home ranges for 9 (5M, 4F) adult mountain lions, resulting in 10 annual and 16 seasonal home range estimates. We found significant differences between estimated 95% home ranges of adult males and adult females using both the BBMM ($F_{1,8} = 14.66$, $P = 0.005$) and MCP methods ($F_{1,8} = 9.22$, $P = 0.016$). Male 95% home ranges averaged 2.1 times larger than for females (male = 231.10 km^2 , 95% CI = $188.19\text{--}274.00 \text{ km}^2$; female = 109.84 km^2 , 95% CI = $70.31\text{--}149.36 \text{ km}^2$) using the BBMM method and 1.8 times larger (male = 348.75 km^2 , 95% CI = $276.90\text{--}420.60 \text{ km}^2$; female = 194.16 km^2 , 95% CI = $139.21\text{--}249.10 \text{ km}^2$) using MCP (Table 1). We found significant differences between the BBMM and MCP home range methods for both males ($t_5 = 5.66$, $P = 0.002$) and females ($t_3 = 7.165$, $P = 0.006$). On average, MCP estimates of 95% home ranges were 51.5% (95% CI = 37.7%–65.4%) larger than BBMM for males, and 81.3% (95% CI = 53.9–108.5%) than BBMM for females. We estimated 50% BBMM annual home ranges of 38.98 km^2 (95% CI = $30.09\text{--}47.87 \text{ km}^2$) for males and 16.86 km^2 (95% CI = $7.04\text{--}26.67 \text{ km}^2$) for females. We found no significant ($F_{1,7} = 2.542$, $P = 0.155$) seasonal variation in 95% BBMM home ranges for adult males (summer = 223.81 km^2 , 95% CI = $167.13\text{--}280.48 \text{ km}^2$; winter = 173.75 km^2 , 95% CI = $141.85\text{--}205.65 \text{ km}^2$), or adult females ($F_{1,6} = 0.872$, $P = 0.386$; summer = 114.09 km^2 , 95% CI = $69.54\text{--}158.64 \text{ km}^2$, winter = 69.40 km^2 , 95% CI = $39.17\text{--}99.63 \text{ km}^2$).

We documented 4 cases of adult male home range overlap, averaging 31.08 km² (range = 15.48–63.32 km²; 13.5% of average annual male home range [231.10 km²]). Percent overlap based upon each individual's annual home range averaged 19.8% (range = 11.0–50.6%); this average included a male who was marked for 2 months and had 50.6% overlap. Excluding this individual, overlap averaged 13.7% (range = 11.0–22.3%). We documented 1 case of intraspecific strife between 2 radio-collared adult males; both males survived the encounter, however, it did result in the failure of 1 radio-collar. Home range overlap in this instance was 29.93 km² accounting for 14.2 % and 50.6% of each individual's home range, respectively; 1 individual was radio-collared for 2 months, which likely overestimated overlap for these animals. Additionally, we observed (via GPS) 2 interactions between a pair of radio-collared males (1 subadult, 1 male); neither interaction resulted in mortality or collar failure.

DISPERSAL MOVEMENTS

We calculated dispersal distances for 5 subadult males and 1 subadult female (Table 2). M107, F108, and F109 were captured as ~10 month old kittens along with their mother F110. F108 became independent from its mother 22 September 2012 at approximately 15 months of age and dispersed 26 days later (Figure 2). F108 traveled 79.10 km (11 weeks post-dispersal) from the capture location before heading back towards its natal range when its collar failed (32 weeks post-dispersal) 5.82 km from its original capture location; it should be noted that F110 had been killed illegally 2 months prior to the return of F108 towards its natal range. In contrast, F109 was not yet independent when it was legally harvested with hounds while traveling with its mother (F110) on 14 December 2012, 1.66 km from original capture location at ~18 months of

age. M107 was not collared but ear-tagged during capture, so exact timing of dispersal and maximum distance from capture site are unknown; however, M107 was seen in the field on 6 June 2013 at ~24 months of age 0.30 km from its capture site and was harvested during the hunting season on 16 November 2013 59.25 km from original capture location at ~29 months of age, making age of dispersal between ~24–29 months. M101 was captured as an independent subadult 14 January 2012 and was illegally trapped 22 March 2012, 21.58 km from its original capture location. M102 was captured as an independent subadult 29 January 2012 and dispersed 12 May 2012, traveling 59.06 km (path distance) over 4 nights before establishing a home range with a centroid 53.98 km from its original capture location.

Two subadult males immigrated into North Dakota from Montana. MT-M3 was originally captured on 2 February 2011 in CMRNWR (R. Matchett, CMRNWR, pers. comm.). MT-M3 was visually captured on trail camera in North Dakota on 20 December 2011 and 22 February 2012, before being harvested during the hunting season on 4 December 2012, 375.87 km from its original capture site. MT-M6 was originally captured and fitted with an Argos GPS collar (TGW-4583H-2, Telonics Inc., Mesa, Arizona, USA) on 28 December 2012 in CMRNWR (R. Matchett, CMRNWR, pers. comm.). MT-M6 began dispersal movements 22 April 2013, crossed into North Dakota 24 July 2013, before being harvested in North Dakota during the hunting season on 28 September 2013, 378.20 km from its original capture location.

SURVIVAL ANALYSIS

We estimated annual survival rates using 15 (8 M; 7 F) radio-collared individuals. MT-M6 was originally captured in Montana but was included in our survival analysis

upon entering North Dakota (via GPS collar data). Due to small sample size, we were unable to look at the effects of age or sex on survival. Our top-ranked model for estimating annual survival included year and late hunting season as covariates. We considered this our top model as it carried the majority of the AICc weight (0.61) and was > 2 AICc lower than the next closest model (Table 3). Estimated annual survival was 64.9% (95% CI = 40.7–83.2%) for 2012 and 17.6% (95% CI = 6.3–40.1%) for 2013; annual survival over the two years of the study was 42.1% (95% CI = 19.6–68.3%).

We recorded 12 mortalities of marked mountain lions during our study; 7 hunter harvest, 2 illegal harvest, 2 removed for depredation, and 1 vehicle collision (Table 4). We also documented 1 case of infanticide; an unmarked kitten was killed and consumed by a radio-collared adult male. Fates of 4 radio-collared are unknown due to collar failure.

DISCUSSION

Our study represents the first research conducted on North Dakota's recently recolonized population of mountain lions in the Little Missouri Badlands. This population occurs on the eastern edge of mountain lion range (LaRue *et al.*, 2012) where environmental conditions (e.g., habitat, prey guilds, anthropogenic influences, land use) vary from western populations and where mountain lions represent the lone large carnivore. Mountain lions persist within a relatively small region of North Dakota where minimum breeding range is estimated at 2,671 km² (Tucker, 2013), less than one third the area of another recently studied Midwestern population (8,400 km² Black Hills, South Dakota; Fecske, 2003). Estimated population size within the region also was relatively

low (Tucker, 2013); thus, our sample of radio-collared individuals represents a considerable proportion of North Dakota's resident mountain lion population.

Adult home ranges of mountain lions occupying the Badlands Region of North Dakota were within the range of previously reported estimates from other studied populations. Our BBMM annual home ranges were on the lower end of previously reported estimates from other regions; however, when using the same methodology (MCP) as these other studies, our estimates were more centrally located within the range of estimates (Table 5). We did not find seasonal shifts in mountain lion home range size or distribution. Previous studies within the Badlands on mule deer (Jensen, 1988; Fox, 1989), as well as a study conducted simultaneously with our research (J. Kolar, University of Missouri, pers. comm.), found no significant seasonal shifts in the size or distribution of mule deer home ranges, the primary prey species of mountain lions in the region (Wilckens *et al.* 2014, in review [Chapter 3]). Lack of seasonal variation in mountain lion home range characteristics is consistent with findings from other studies conducted in regions with non-migratory ungulate prey (*e.g.*, Grigione *et al.*, 2002; Sweanor, 1990; Ross and Jalkotzy, 1992).

Home range analysis using BBMM excluded larger areas typically avoided by mountain lions (*e.g.*, open grasslands, pastures, agricultural fields, and oil wells) in comparison to MCP. The MCP method significantly overestimated ($\bar{x} = 63.4\%$, range = 36.1–109.6%) annual home ranges for individuals in comparison to BBMM, especially those with irregularly shaped home ranges, by including large regions that were never traversed. Further analysis of habitat use (selection/avoidance) would be prudent given the region's potential for future habitat alterations (*e.g.*, oil and gas development).

Previous studies have reported varied levels of male home range overlap ranging from non-existent (Spreadbury *et al.* 1996), moderate (12.0–20.0%, Ross and Jalkotzy, 1992), or substantial (49.8%, Logan and Sweanor, 2001). Our estimates of adult male home range overlap (13.7%) were moderate; however, our estimates could be biased low due to the spatial distribution of our radio-collared animals. Some males were completely surrounded by other marked males, yet others only had adjacent radio-collared males in one direction. The pattern of male home ranges across the landscape made it evident that there likely were unmarked resident males between some of our radio-collared individuals; confirmations of unmarked males through trail camera photos and harvest data provided additional evidence of potential male home range overlap that was not accounted for in our estimates. Underestimating home range overlap has the potential to decrease estimates of both population densities and population size within the region.

Immigration of mountain lions into North Dakota from the Black Hills, South Dakota has been reported in a previous study (Thompson and Jenks, 2010). However, our study was the first to record immigration into the Badlands from Montana; we documented the long distance dispersal of 2 subadult males from CMRNWR in eastern-central Montana (R. Matchett, CMRNWR, pers. comm.). We documented dispersal within the Badlands and immigration into the region, but did not record any emigration from the Badlands population; however, recent genetic research has documented individuals from North Dakota occurring within the Black Hills, South Dakota (R. Juarez, South Dakota State University, pers. comm.). Straight-line dispersal distance has been used as an index of movement; however, it may underestimate landscape movement

patterns and potential consequences of those movements (*e.g.*, varying survival across different habitats encountered during dispersal). Impacts of these dispersal movements on mountain lion population dynamics in North Dakota remain unknown.

Overall survival rate (42%) was considerably lower in our study area than those published from other hunted populations in Washington (65%, Robinson *et al.*, 2008), Utah (74%, Lindzey *et al.*, 1988; 64%, Stoner *et al.*, 2006), Oregon (57–86%, Clark *et al.*, 2014), Alberta (86–97%, Ross and Jalkotzy, 1992; 67%, Knopff *et al.*, 2010), and the Pacific Northwest ([Idaho/Washington/British Columbia] 59%, Lambert *et al.*, 2006). Sport hunting was the greatest cause of mortality in our study area, typical of hunted populations (*e.g.*, Stoner *et al.*, 2006; Robinson *et al.*, 2008); however, comprehension of all mortality factors within a population is essential for a true understanding of population dynamics. This may be difficult as some causes of mortality are not readily documented and consequently may be underestimated in unstudied populations. We did not find any cases of mortality resulting from disease or starvation; however, mortalities related to both disease (Florida, Taylor *et al.*, 2002; Utah, Logan and Sweanor, 2001, Stoner *et al.*, 2006; South Dakota, Jansen, 2011) and starvation (Utah, Lindzey *et al.*, 1988, Logan and Sweanor 2001; South Dakota, Jansen, 2011) have been reported in other regions.

Incidences of intraspecific strife resulting in the death of 1 or multiple participants would not likely be documented unless animals involved are being actively monitored. Previous research reported lower levels (% of total mortality) of mortality due to strife in hunted populations (17–18%, Stoner *et al.*, 2006; 16%, Jansen 2011) compared to un hunted populations (46–53%, Logan and Sweanor 2001), suggesting partial compensation (Quigley and Hornocker, 2009). We did not document any mortalities as a

result of intraspecific strife; however, we observed 3 interactions between males (not resulting in mortality) and captured multiple other adult males with facial and body scarring, indicating previous encounters with other individuals. We documented only 1 incidence of infanticide; however, we had anecdotal evidence that it occurs more often. For example, we observed a collared female breeding with an ear-tagged male only a month after observing her with a ~7–8 month old kitten; it is reasonable to suggest that this male may have been involved with the loss of this kitten. Data on kitten survival in North Dakota is currently nonexistent, and further research is needed to quantify its impact on the population.

Some human-caused mortalities (*e.g.*, intentional poaching, incidental snaring/trapping, road-kill) are likely underestimated in North Dakota due to under- or non-reporting of these types of events. Out of season harvest within the Little Missouri Badlands (17% of mortalities) was higher than reported for other hunted populations (6%, Stoner *et al.*, 2006, 7%, Jansen, 2011). In addition to intentional illegal harvest, 2 marked mountain lions also were incidentally caught in neck snares, though neither died. One ear-tagged mountain lion (M107) was captured in a legally set snare, was released alive by the trapper, and survived until being harvested the following hunting season. The second individual (M103) was captured in an illegally set snare (no breakaway device) and broke the snare cable; this individual was recaptured by researchers with the snare around its neck and would have likely died had the radio-collar not kept the snare from closing. Two additional individuals (1 captured by researchers, 1 captured on trail camera) were observed with a thin ring of white hair around their neck, indicating a past encounter with a neck snare; M107 had this same trait when it was harvested 11 months

after being snared and released. Knopff *et al.* (2010) observed 33% of mortality events resulted from incidental snaring of mountain lions in Alberta, and found a correlation between increasing numbers of mountain lions snared and increasing numbers of wolves snared. In North Dakota, impacts of snaring on mountain lion survival likely fluctuate with fur prices of targeted species (*e.g.*, bobcat, coyote) and weather conditions (*e.g.*, snow depth [allowing or preventing access for trappers]). Although some cases of incidental capture were reported by the individuals responsible, we also found multiple cases where incidental capture or illegal harvest would not have been documented had the mountain lions involved not been actively monitored (*i.e.*, radio-collared). Despite North Dakota's regulations regarding killing mountain lions for protection of property, we documented 1 instance where a landowner shot a radio-collared mountain lion for this purpose, but did not report it until questioned by officials. This leads us to question how many individuals are being shot/snared/trapped and not reported. Not accounting for these mortality events can lead to overestimation of the population's survival rates.

Regulated harvest seasons can have varied impacts on mountain lions within the Badlands. Hunting mountain lions without hounds (*e.g.*, North Dakota's early season) is largely opportunistic and therefore, involves little hunter selection (Anderson *et al.*, 2009); hunters are likely to harvest at the first opportunity for success. This may lead to increased female take due to higher abundance on the landscape (Martello and Beausoleil, 2003). Although females accompanied by spotted kittens are protected from harvest in North Dakota (Tucker, 2013), they often travel without young and are susceptible to harvest (Barnhurst and Lindzey 1989); thus, hunting also may have indirect effects on survival. During our study, 2 radio-collared females who had dependent

young, but were traveling without them, were legally harvested during hunting season. Anderson *et al.* (2009) suggested that hound hunting (*e.g.*, North Dakota's late season) likely results in the increased take of males due to their longer travel distances, which may increase the chance that hunters find their tracks; hound hunters also have time underneath a treed mountain lion to observe it and may choose to pass on females. However, hound hunting is still relatively new within North Dakota; anecdotal evidence via personal communication with hunters indicated that the majority of houndsmen take the first mountain lion they are able to bay. Additionally, due to the lack of large trees in the region, most mountain lions pursued with hounds in North Dakota are bayed in holes, providing limited chances, compared to a treed animal, for hunters to positively identify sex (track identification only). Not accounting for all causes of mortality, and their varying impacts, has the potential to alter estimates of survival within the region.

Our research on this previously unstudied mountain lion population has provided valuable insight on population characteristics within the region. Our home range estimates will allow for more refined estimates of distribution, minimum breeding range, and population size and density. Survival rates and dispersal characteristics have additional implications for population dynamics; our research was the first to estimate mountain lion survival within North Dakota and also documented a novel source of immigration into the region. Our study provides region-specific population characteristics of a newly recolonized mountain lion population within the Little Missouri Badlands and will serve as baseline data for future studies in North Dakota.

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Mountain lion (*Puma concolor*) feeding behavior in the recently recolonized

Little Missouri Badlands, North Dakota. J. Mammal.

Table 1.—Mean annual home range size ($\text{km}^2 \pm$ standard errors) of male and female mountain lions (*Puma concolor*) in North Dakota, 2012–2013.

	<u>BBMM^a</u>		<u>MCP^b</u>	
	95%	50%	95%	50%
Male	231.10 \pm 21.89	38.98 \pm 4.53	348.75 \pm 36.66	114.30 \pm 22.04
Female	109.84 \pm 20.17	16.86 \pm 10.02	194.16 \pm 28.03	57.86 \pm 11.14

^aBrownian bridge movement model

^bMinimum convex polygon

Table 2.—Straight-line dispersal distance and dispersal age of mountain lions (*Puma concolor*) in North Dakota, 2011–2013.

Mountain Lion ID	Sex	Capture Date	Began Dispersal	End Dispersal	Dispersal Age	Distance From Capture Site (km)	Endpoint	Method
MT–M3	M	2/2/2011	Post 3/8/2011 ^a	12/20/2011 ^b	~2.5 yrs	375.9	Mortality	Ear-tag
MT–M6	M	12/28/2012	4/22/2013	9/28/2013	~2.5 yrs	378.2	Mortality	GPS collar
M101	M	1/14/2012	1/14/2012	3/22/2012	~1.5–2 yrs	21.6	Mortality	GPS collar
M102	M	1/29/2012	5/12/2012	5/16/2012	~2.5 yrs	54.0	HR centroid	GPS collar
M107	M	4/26/2012	Post 6/6/2013 ^c	11/16/2013	~2–2.5 yrs	59.3	Mortality	Ear-tag
F108	F	4/26/2012	10/18/2012	5/3/2013	~15 mo	5.8 ^d	Collar Failure	GPS collar
F109	F	4/26/2012	–	–	Had not dispersed at ~18 mo	1.7	Mortality	GPS collar

^aMT–M3 last heard via VHF by Charles M. Russell National Wildlife Refuge staff.

^bMT–M3 first captured on trail camera within Little Missouri Badlands, North Dakota, >16 km from mortality (12/4/2012) location.

^cM107 observed in the field 0.3 km from original capture location.

^dF108 maximum straight-line distance from original capture location = 79.1 km, collar failure 5.8 km from capture location.

Table 3.—The top 5 models for estimating mountain lion (*Puma concolor*) survival in North Dakota, 2012–2013.

Model Description	K	AICc	Δ AICc	AICc Weight	Model Likelihood	Deviance
Year ^a + Late_hunt ^b	3	59.842	0.000	0.605	1.000	53.682
Late_hunt	2	61.857	2.015	0.221	0.365	57.778
Early_hunt ^c + Late_hunt	3	63.330	3.488	0.106	0.175	57.170
Year + Total_hunt ^d	3	65.815	5.973	0.031	0.051	59.655
Total_hunt	2	67.120	7.278	0.016	0.026	63.041

^aYear = calendar year (2012, 2013)

^bLate_hunt = late mountain lion hunting season (hound use permitted), NDGFD Zone 1

^cEarly_hunt = early mountain lion hunting season (hound use prohibited), NDGFD Zone 1

^dTotal_hunt = combined early and late mountain lion hunting seasons, NDGFD Zone 1

Table 4.—Cause-specific mortality ($n = 12$) of marked mountain lions (*Puma concolor*) in North Dakota, 2012–2013.

Cause	Males		Females		Total	%
	Ad	Subad	Ad	Subad		
Hunter harvest	2	2	2	1	7	58
Illegal harvest		1	1		2	17
Depredation	2				2	17
Vehicle collision	1				1	8
Total	5	3	3	1	12	
%	42	25	25	8		

Table 5.— Reported annual home range sizes (km²) of male and female mountain lions (*Puma concolor*).

Study	Study Area	Method	Male HR (km ²)	Female HR (km ²)
Seidensticker <i>et al.</i> , 1973	Idaho	MCP ^a	453	233
Hemker <i>et al.</i> , 1984	Utah	MCP	826	685
Ross and Jalkotzy, 1992	Alberta	MCP	334	140
Beier and Barrett, 1993	California	MCP	767	218
Logan and Sweanor, 2001	Utah	MCP	188	72
Dickson and Beier, 2002	California	85% fixed kernel	470	81
Thompson, 2009	South Dakota	90% adaptive kernel	641	140
This study	North Dakota	MCP	349	194
This study	North Dakota	BBMM ^b	231	110

^aMinimum convex polygon.

^bBrownian bridge movement model.

FIGURE 1.—Our study area was focused within the Little Missouri Badlands of western North Dakota from 2011–2013.

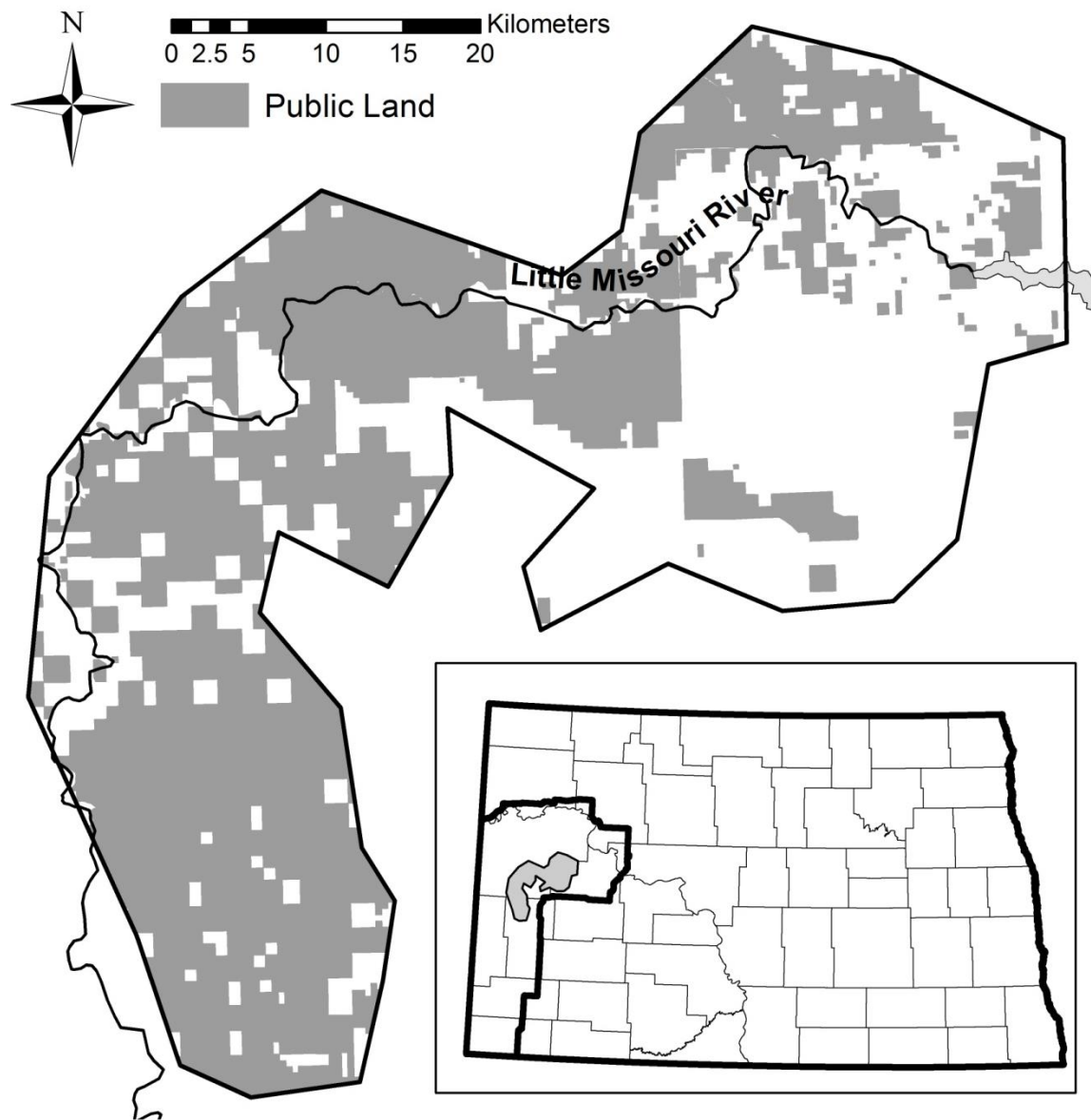
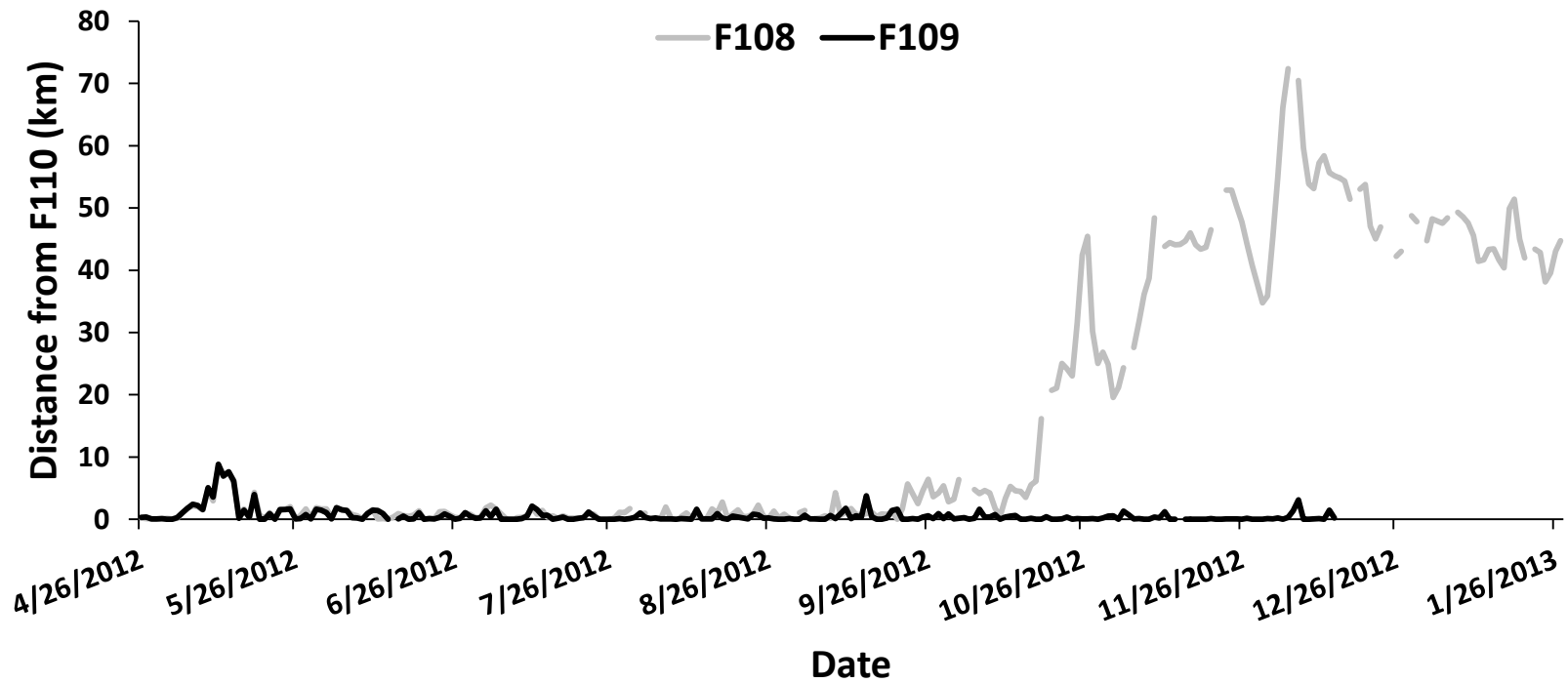


Figure 2.— Daily distance (km) of 2 mountain lions (*Puma concolor*; F108, F109) from their mother (F110), from capture (4/26/2012; ~10 mo) until death (F109 [12/14/2012]; F110 [1/26/2013]). F108 became independent of F110 at ~15 mo and dispersed 26 days later.



**CHAPTER 3: MOUNTAIN LION (*Puma concolor*) FEEDING
BEHAVIOR IN THE RECENTLY RECOLONIZED LITTLE
MISSOURI BADLANDS, NORTH DAKOTA**

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coauthored by Joshua B. Smith, Stephanie A. Tucker, Daniel J. Thompson, and Jonathan
A. Jenks.*

**Mountain lion (*Puma concolor*) feeding behavior in the recently recolonized Little
Missouri Badlands, North Dakota**

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Recent recolonization of mountain lions (*Puma concolor*) into the Badlands of North Dakota, USA, has led to questions regarding the potential impacts of predation on prey populations in the region. From 2012–2013, we deployed 9 real-time global positioning system (GPS) collars to investigate mountain lion feeding habits. We monitored mountain lions for 1,845 days, investigated 506 GPS clusters, and identified 292 feeding events. Deer (*Odocoileus* spp.) were the most prevalent item in mountain lion diets (76.9%). We used logistic regression to predict feeding events and size of prey consumed at an additional 535 clusters. Our top model for predicting presence of prey items produced a receiver operating characteristic (ROC) score of 0.90 and an overall accuracy of 81.4%. Application of our models to all GPS clusters resulted in an estimated ungulate kill rate of 1.09 ungulates/week (95% CI = 0.83–1.36) in summer and 0.90 ungulates/week (95% CI = 0.69–1.12) in winter. Estimates of total biomass consumed were 5.8 kg/day (95% CI = 4.7–6.9) in summer and 7.2 kg/day (95% CI = 5.3–9.2) in winter. Overall scavenge rates were 3.7% in summer and 11.9% in winter. Prey composition included higher proportions of nonungulates in summer (female = 21.54%;

male = 24.80%) than in winter (female = 4.76%; male = 7.46%). Proportion of juvenile ungulates in mountain lion diets increased following the ungulate birth pulse in June (June–August = 60.67%, 95% CI = 43.01–78.33; September–May = 37.21%, 95% CI = 30.76–43.65), resulting in an ungulate kill rate 1.61 times higher during the fawning season (1.41 ungulates/week, 95% CI = 1.12–1.71) than during the remainder of the year (0.88 ungulates/week, 95% CI = 0.62–1.13). Quantifying these feeding characteristics is essential to assessing the potential impacts of mountain lions on prey populations in the North Dakota Badlands, where deer dominate the available prey base and mountain lions represent the lone apex predator.

Key words: Badlands, cougar, food habits, global positioning system (GPS) collars, kill rate, mountain lion, North Dakota, predation, *Puma concolor*

Quantifying kill rates, consumption rates, and composition of prey (e.g., species, age, sex, etc.), and understanding the ecological factors (e.g., competing predators, available prey guilds, population structure, season) that may cause them to vary, is vital in assessing potential impacts of mountain lions (*Puma concolor*) on prey populations (Sand et al. 2008, Knopff and Boyce 2007, Knopff et al. 2009). Although numerous studies have been published on mountain lion feeding habits in North America, reported predation rates have varied based upon study area and methods used (see Knopff et al. 2010: Table 1). Prior to the introduction of global positioning system (GPS) collars, estimates of predation were obtained primarily via intensive snow-tracking (Hornocker 1970), radio-tracking (Cooley et al. 2008, Murphy 1998, Nowak 1999), or energetic models (Ackerman et al. 1986, Hornocker 1970, Laundré 2005). However, these methods have distinct limitations as they tend to provide small sample sizes, and are often restricted by

season or weather (e.g., snow, flying conditions), which requires extrapolation of findings to other seasons (Sand et al. 2008). These techniques also potentially underestimate the importance of smaller prey items in the diet due to shorter handling times (Webb et al. 2008). All of these factors have the potential to increase bias and decrease precision when estimating basic parameters such as kill rates (Knopff et al. 2010, Sand et al. 2008). More recent studies have employed GPS collars to aid in monitoring large carnivore predation (Anderson and Lindzey 2003, Knopff et al. 2010, Miller et al. 2013, Webb et al. 2008), allowing efficient monitoring of more individuals over longer, continuous periods, across all seasons, leading to increased precision in predation estimates.

Previous studies have demonstrated that the presence of other large carnivores can affect feeding habits of mountain lions (Bartnick et al. 2013, Kortello et al. 2007, Murphy et al. 1998). Mountain lions represent the only large carnivore in the North Dakota Badlands, a factor that distinguishes this system from other predation studies conducted in multi-predator systems (e.g., Knopff et al. 2010, Ruth et al. 2010). Additionally, variation in available prey types, habitat conditions, and anthropogenic influences among study areas further limits the extrapolation of mountain lion feeding rates to other populations/regions, even when the most rigorous methods are used (e.g., Knopff et al. 2010).

Mountain lions have recently recolonized western North Dakota (North Dakota Game and Fish Department 2006) and persist in a semi-isolated population separated from other established breeding populations by vast expanses of grasslands that comprise the Northern Great Plains; although, immigration into North Dakota has been documented from neighboring populations in Montana (R. Matchett, Charles M. Russell

National Wildlife Refuge, personal communication) and the Black Hills of South Dakota (Thompson and Jenks 2005). We documented mountain lion predation in the unique environment of the North Dakota Badlands using GPS collars to evaluate 5 research questions: 1) what is the prey composition of mountain lion diets, 2) how many ungulates do mountain lions kill, 3) what effect does scavenging have on ungulate consumption rates, 4) what effect does season have on mountain lion feeding habits, and 5) what effect does demographic status have on mountain lion feeding habits?

MATERIALS AND METHODS

Study Area.—We studied mountain lion predation in western North Dakota, USA, within Billings, Dunn, and McKenzie counties. Our 2,050 km² study area comprised approximately one third of the Little Missouri Badlands Region, and was contained within “Zone 1” of the mountain lion hunting area, as defined by the North Dakota Game and Fish Department (Figure 1). The Badlands Region is characterized by highly eroded, steep clay canyons and buttes, distributed along the Little Missouri River and ranging in elevation from approximately 570 m to 710 m above mean sea level (Hagen et al. 2005). Vegetation occurring in draws of the northern and eastern slopes was predominately Rocky Mountain juniper (*Juniperus scopulorum*) and green ash (*Fraxinus pennsylvanica*), while riparian areas contained cottonwood (*Populus deltoides*) stands. Southern and western slopes, plateaus, and bottomlands were often barren or contained short-grass prairie (Hagen et al. 2005). Grass species within the region included blue grama (*Bouteloua gracilis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), Indian ricegrass (*Achnatherum hymenoides*), western wheatgrass (*Pascopyrum smithii*), and little bluestem (*Schizachyrium scoparium*; Hagen et al. 2005). The Killdeer Mountains

Region also was located within the study area, and represented a 60 km² island of elevated habitat connected to the Badlands Region by a few small drainages. This area rises 300 m above the surrounding prairie to 1,010 m and is comprised of a mosaic of open grassland and deciduous species, including green ash, quaking aspen (*Populus tremuloides*), burr oak (*Quercus macrocarpa*), paper birch (*Betula papyrifera*), western black birch (*Betula niger*), and American elm (*Ulmus americana*), with a dense undergrowth of beaked hazelnut (*Corylus cornuta*; Hagen et al. 2005).

North Dakota's climate is continental; a relatively dry climate (42.7 cm mean annual precipitation) characterized by hot summers (record high 49°C) and cold winters (record low -51°C; Seabloom 2011). Cattle grazing was the most common land use in the Badlands; however, oil and gas development was rapidly increasing within the region (Hagen et al. 2005). Our study area was a mosaic of public (49%) and private land (51%), with the western portion predominately public and the eastern portion predominately private (Figure 1). Public lands within the study area included Theodore Roosevelt National Park (TRNP), the Little Missouri National Grasslands, Bureau of Land Management properties, North Dakota State Trust lands, and the North Dakota Game and Fish Department Killdeer Wildlife Management Area.

Potential ungulate prey for mountain lions included mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*), and pronghorn (*Antilocapra americana*); bison (*Bison bison*) were potential prey within TRNP. Potential nonungulate prey included beaver (*Castor canadensis*), porcupine (*Erethizon dorsatum*), turkey (*Meleagris gallopavo*), and raccoon (*Procyon lotor*). Domestic livestock (e.g., cattle, horses, goats) also were available as prey. Other

carnivores including coyote (*Canis latrans*), bobcat (*Lynx rufus*), and red fox (*Vulpes vulpes*), were present as both potential competitors of and prey items for mountain lions.

Capture and monitoring.—From 2011–2013 we captured mountain lions from established bait (e.g., roadkilled ungulates) sites with the use of foot-hold traps and foot-hold snares (Logan et al. 1999). We immobilized mountain lions with a mixture of tiletamine and zolazepam (Telazol; 5.0 mg/kg) and xylazine (Anased; 1.0 mg/kg; Kreeger and Arnemo 2007) based on estimated live animal body weight via dart rifle (Dan-Inject, Børkop, Denmark, EU). We weighed, measured, determined sex, and estimated age (using tooth wear and pelage characteristics [Anderson and Lindzey 2000]) of captured mountain lions. We classified mountain lions as kittens (dependent on mother), subadults (dispersal until 2.5–3 yrs), or adults (>3 yrs) and fitted independent mountain lions (i.e., not dependent on adult female) with real-time GPS radiocollars (Advanced Telemetry Systems [ATS] G2110E, Isanti, Minnesota, USA). Upon completion of handling, we administered 0.125 mg/kg yohimbine to reverse xylazine, released mountain lions on site, and monitored them from a distance to ensure safe recovery (Kreeger and Arnemo 2007). All procedures were approved by the South Dakota State University Animal Care and Use Committee (Approval number 11–080A) and followed recommendations of the American Society of Mammalogists (Sikes and Gannon 2011).

We programmed GPS collars to collect 8 locations/day (0000, 0300, 0600, 0900, 1200, 1500, 1800, and 2100 hrs). Collars were set to attempt a GPS fix for 120 seconds at each scheduled fix time (ATS “forest” setting), then transmit those coordinates via satellite every 24 hrs to an automated email system. We used a Python script (Python software Foundation, Hampton, New Hampshire, USA) developed by Knopff et al.

(2009) to identify potential feeding sites from independent subadult and adult mountain lions. We considered a cluster (i.e., a potential feeding site) as ≥ 2 GPS locations within 200 m over a 6-day period. Once clusters were identified, we downloaded all GPS locations associated with the cluster into a hand-held GPS unit (Garmin International, Olathe, KS) and visited clusters as soon as possible to determine possible predation events. We conducted a systematic search at each cluster by walking 5–10 m wide (depending on visibility) zig-zag patterns at each location out to 30 m from the center of the cluster. A concurrent study (Smith et al., In Review), found a low probability of 2 location clusters containing kills (1 probable ungulate kill out of 237 clusters investigated; 0.4%) outside of the fawning season (May–August). Therefore, we visited clusters containing ≥ 2 locations from May–August and those containing ≥ 3 locations from September through May.

Characteristics of prey.—We categorized prey remains found at cluster sites as either a predation or scavenging event provided there was evidence the mountain lion had killed or fed on the carcass. Our default category was to classify prey remains as a probable mountain lion kill, provided the age of prey remains closely matched the dates over which the cluster was created and there was no evidence to contradict the occurrence of mountain lion predation. We classified clusters as scavenging events in cases where it was clear the cause of death (e.g., hunter harvest, road-kill, carcass dump site) was not due to the mountain lion assigned to that cluster or if the carcass age greatly preceded cluster dates (Knopff et al. 2010).

We identified prey species and sex by anatomical characteristics (e.g., tail, metatarsal glands, antlers), and determined age from tooth eruption and wear

(Severinghaus and Cheatum 1956). In cases where we could not determine species, sex, or age, carcasses were classed as “unknown”. We assigned each predation event to either summer (15 May–14 November) or winter (15 November–14 May) based on time of the first GPS location in the cluster. Seasonal cutoffs were chosen to ensure we encapsulated the ungulate birth pulse within one season (Knopff et al. 2010).

We calculated species composition by percent frequency seasonally for male and female mountain lions. We compared proportions of ungulate and nonungulate prey in diets and percentage of prey scavenged, by mountain lion sex and season (winter/summer) using chi-square tests. We compared proportions of juvenile ungulates in diets of all mountain lions during fawning (June–August) and non-fawning periods (September–May) using a single-factor analysis of variance. We performed these analyses using SYSTAT 11.0 (Systat Software Inc., Chicago, Illinois, USA).

To estimate biomass (kg) consumed, we assigned approximate live weights to adult (≥ 2 yrs) ungulate prey based on published estimates (Table 1). For elk and deer (white-tailed and mule deer combined), we assigned weights to adults based on those from Jensen (2000). For bighorn sheep, we assigned values based on known weights from the Black Hills, South Dakota (J. B. Smith, South Dakota State University, unpublished data). To estimate yearling and young of the year ungulate biomass, we used a von Bertalanffy growth equation modified from Knopff et al. (2010). For example, we used an inflection point (I) of 140 days (Knopff et al. 2010) and adjusted the growth rate (K) until birth weights approximated known ungulate birth weights for the region (e.g., Smith et al. 2014). We then assigned median weights for each of 4 juvenile age classes (0–3 months, 3–6 months, 6–12 months, and 12–24 months; Table 1). When

we could not determine age class, we assigned yearling weight to the kill (Knopff et al. 2010). When we could determine that the prey was an adult but were unable to determine sex, we assigned the average adult weight (i.e., [ad M + ad F]/2; Knopff et al. 2010). For nonungulate prey, we did not differentiate between sex or age class; instead, we assigned mean weights provided in Seabloom (2011) for mammals and Dunn and Alderfer (2006) for birds. As it was often difficult to ascertain the amount of biomass consumed at scavenge sites, we used predictions from our large- vs small-prey model (see below) to assign scavenge events to one of the 2 categories. We then applied the average biomass from all known small-prey kills or large-prey kills to each scavenged item within the same respective category.

Model development.—We attempted to census mountain lion predation of ungulates throughout the monitoring period for each marked mountain lion by visiting all generated GPS clusters. However, not all clusters could be investigated (e.g., limited private property access); therefore, we used multivariate logistic regression (Hosmer and Lemeshow 2000) to predict predation events at non-investigated clusters. First, we developed a model using the *lme4* package (Bates et al. 2014) in Program *R* to predict presence/absence of prey items ≥ 4 kg using data from investigated clusters where collar fix success was $\geq 45\%$ (Knopff et al. 2009). We removed clusters associated with the initial radio-collaring, collar removals, and den sites prior to modeling. We used season (summer and winter) and 8 variables generated from our Python script for model development: 1) number of locations in clusters, 2) fidelity (number of locations in the cluster minus number of locations away from cluster during cluster duration), 3) hours (number of hours between the first and last location in the cluster), 4) days (number of

24-hour periods in which at least one location was collected within the cluster), 5) night points (total number of locations within the cluster that were obtained between 1800–0600 hrs), 6) night proportion (number of night locations in cluster divided by total number of locations in cluster, 7) average distance (average distance that each cluster location was from cluster centroid), and 8) cluster radius (difference between cluster centroid and the farthest location within the cluster).

After testing for correlation between variables ($r \geq 0.7$; SYSTAT 11.0), we developed a priori models using uncorrelated variables, and fit them to our investigated GPS clusters. We assessed model fit using Akaike's Information Criteria (AIC; Burnham and Anderson 2002). We applied coefficients from our top regression model to our investigated cluster data to calculate a prediction value for each cluster. We then used a receiver operating characteristic (ROC) curve generated in package *ROCR* (Sing et al. 2005) in Program *R* to determine an optimal cutoff value for our model predictions (Boyce et al. 2002, Knopff et al, 2009, Miller et al. 2013). Selection of cutoff values was imperative for optimal prediction performance of the model (Knopff et al. 2009, Merrill et al. 2010, Miller et al. 2013, Webb et al. 2008). Selecting a cutoff that maximizes the true positive rate, or sensitivity, may lead to an overestimation of kill rate due to an increased number of false positives generated by the model. However, maximizing the true negative rate, or specificity, may lead to an underestimation of kill rate by misclassifying many sites as not having a ≥ 4 kg prey item present. We chose our cutoff values by maximizing the overall model accuracy, defined as the sum of the true positive predictions and true negative predictions, divided by the sum of actual positive and negative clusters (Sing et al. 2005).

We developed a second logistic model using this same methodology to further predict if clusters contained large ($\geq 32\text{kg}$) or small ($< 32\text{kg}$) prey items. We used 32 kg as a cut point to separate classes, allowing deer fawns ≥ 6 months of age to be incorporated as large prey items. We applied our top regression models to non-investigated GPS clusters and categorized them as no-prey, large prey, or small prey. We assigned a consumption category (ungulate kill, nonungulate kill, scavenge) to non-investigated clusters based upon percentage of each category found at investigated clusters within the same prey-size class and season (e.g., large prey, winter) as the predicted cluster. We estimated a predicted biomass value for each non-investigated cluster based upon the average biomass from investigated clusters within the same prey-size class, and season.

Feeding rates.— For mountain lions fitted with GPS collars that had $\geq 45\%$ fix success and were monitored for ≥ 28 days within a given season and demographic class (Knopff et al. 2010), we calculated 3 feeding rates: 1) ungulate kill rate, using feeding events where we determined that the ungulate prey was killed by the mountain lion that generated the cluster, 2) ungulate consumption rate, using both mountain lion-killed ungulates and scavenged ungulates, and 3) biomass consumed, including all ungulate and nonungulate prey items consumed. We used a ratio estimator to calculate feeding rates using total number of weeks (or days for biomass) monitored as the denominator and total number (actual + predicted) of ungulate kills, ungulate consumptions, or prey biomass as the numerator (Knopff et al. 2010).

We used all 3 rates to estimate annual feeding rates of mountain lions by using individuals as the unit of analysis and pooling data across season and demographic class.

We also calculated seasonal feeding rates for 3 demographic classes: female (F), male (M), and adult female with young (family group [FG]). We calculated multiple feeding rates for individual mountain lions if they transitioned between classes during our study. We assessed the effects of demographic class on feeding rates using a single-factor analysis of variance for each season (SYSTAT 11.0). Demographic and season-specific feeding rates were the unit of analysis.

RESULTS

We monitored predation of 9 GPS-collared mountain lions for 1,845 days ($\bar{x} = 205$ days/mountain lion, $SD = 116.55$) across summer (1,029 days) and winter (816 days) seasons from July 2012 to July 2013. Our sample of GPS collared mountain lions included 4 adult females, 1 subadult male, and 5 adult males (1 of which was collared as a subadult but transitioned to adult during the study). GPS collars averaged 77% fix success during our monitoring period (range = 67–90%). We visited 506 GPS clusters and documented 292 feeding events. We visited cluster sites an average of 14.86 days ($SD = 13.14$) after the first date of the cluster. We were able to identify species at 251 (86.0%) clusters (100.0% positively identified when combining mule deer and white-tailed deer), age of carcass at 252 (86.3%) clusters, and sex of carcass at 117 (40.1%) clusters. Due to complete consumption prior to investigation of the cluster, differentiation of deer species and sex was difficult for juvenile ungulates within the first few months postpartum.

Prey composition.—We documented 12 unique species of prey items at mountain lion feeding sites. Ungulates (mule deer, white-tailed deer, elk, and bighorn sheep) comprised the majority of identified prey items found based on relative frequency

(80.9%). Deer (*Odocoileus* spp.) were the most prevalent (76.9%) prey and at clusters where we could identify deer species ($n = 189$), mule deer were most common (85.7%), accounting for 54.2% of mountain lion diets. White-tailed deer (9.0%), bighorn sheep (2.7%), and elk (1.3%) occurred at lower frequencies. Other prey items included beaver (6.7%), porcupine (5.0%), coyote (1.7%), raccoon (1%), turkey (1%), and domestic cattle (1%) with the remainder of species (mountain lion, cottontail [*Sylvilagus* spp.]) occurring at <1% (Table 2). Scavenged prey accounted for 6.7% based on relative frequency of prey items.

We observed significant seasonal variation in prey composition (ungulate/nonungulate distribution) for both sexes (female, $\chi^2_1 = 14.347$, $P < 0.001$; male, $\chi^2_1 = 11.591$, $P = 0.001$); however, prey composition was similar between sexes ($\chi^2_3 = 1.136$, $P = 0.768$) throughout both seasons. Mountain lions consumed higher proportions of nonungulate prey in summer (females = 21.5%; males = 24.8%) than winter (females = 4.8%; males = 7.5%). Scavenge frequencies for both sexes were higher in winter (females = 11.9%; males = 11.9%) than in summer (females = 3.1%; males = 4.0%; Table 2).

Model performance.—We used logistic regression to predict predation events for 535 clusters. The top model for predicting consumption of prey ≥ 4 kg at GPS clusters included hours, average distance, night proportion, season, and fidelity as covariates. This model had an AIC score that was 2.34 AIC less than the second ranked model and carried 56.1% of the AIC weight (3.22 times more AIC weight than the second ranked model; Table 3). Prey carcasses were more likely to be present at clusters in summer with a higher number of hours between first at last locations at the cluster, smaller

average distance from cluster locations to cluster centroid, higher proportion of night time locations within the cluster, and higher site fidelity (Table 4). This model fit the data well (Hosmer and Lemeshow 2000), producing a ROC area under the curve (AUC) of 0.90. We used a cutoff value of 0.53 resulting in a maximized overall model accuracy of 81.4%. The resulting model predicted consumption of prey items at 62 of 535 (11.6%) non-investigated clusters.

Our top model for differentiating large and small prey items included days, season, and fidelity as covariates. This model had an AIC score that was 2.73 Δ AIC less than the second ranked model and carried 60.9% of the AIC weight (3.93 times greater than the second ranked model; Table 5). Large carcasses were more likely to be present at clusters in winter when fidelity and number of days a mountain lion was present at the cluster increased (Table 4). This model fit the data well (Hosmer and Lemeshow 2000), producing a ROC curve with an AUC value of 0.89. We used a cutoff value of 0.55 resulting in a maximized overall model accuracy of 84.6%. Of the 62 non-investigated clusters that were previously predicted to have a prey item consumed, our second model predicted 24 (38.7%) clusters to contain large carcasses and 38 (61.3%) to contain small carcasses.

Feeding Rates—Overall ungulate kill rate, not accounting for seasonal or demographic effects, was 1.01 ungulates/week (95% CI = 0.76–1.27), total ungulate consumption rate was 1.11 ungulates/week (95% CI = 0.87–1.35), and total biomass consumed was 6.55 kg/day (95% CI = 5.07–8.20). Summer ungulate kill rates (1.09 ungulates/week, 95% CI = 0.83–1.36) were similar ($F_{1,15} = 1.326$, $P = 0.268$) to winter rates (0.90 ungulates/week, 95% CI = 0.69–1.12). Ungulate consumption rates also were

similar ($F_{1,15} = 0.742$, $P = 0.403$) for summer (1.15 ungulates/week, 95% CI = 0.91–1.40) and winter (1.03 ungulates/week, 95% CI = 0.83–1.24). Total biomass consumed/day was similar ($F_{1,15} = 2.053$, $P = 0.172$) for summer (5.81 kg/day, 95% CI = 4.71–6.90) and winter (7.24 kg/day, 95% CI = 5.25–9.22).

We documented a difference ($F_{1,14} = 4.237$, $P = 0.059$) in ungulate kill rates during the fawning period (June–August) compared with the remainder of the year. Ungulate kill rate was 1.61 times higher during the fawning period (1.41 ungulates/week, 95% CI = 1.12–1.71) than during the remainder of the year (0.88 ungulates/week, 95% CI = 0.62–1.13). Increase in ungulate kill rate during the fawning period occurred simultaneously to increase in reliance on juvenile prey ($F_{1,14} = 4.959$, $P = 0.043$; fawning period = 60.67%, 95% CI = 43.01–78.33; non-fawning period = 37.21%, 95% CI = 30.76–43.65). Despite increase in ungulate kill rate, total biomass consumed did not vary ($F_{1,14} = 0.026$, $P = 0.873$; fawning period = 6.73 kg/week, 95% CI = 4.20–9.25; non-fawning period = 6.90 kg/week, 95% CI = 4.41–9.39). Furthermore, when we removed August from the ungulate fawning period, and compared only June and July to the remainder of the year, we noted an even greater difference ($F_{1,14} = 5.2$, $P = 0.039$) in ungulate kill rate. Ungulate kill rate was 1.68 times higher during June and July (1.52 ungulates/week, 95% CI = 1.26–1.78) than the remainder of the year (0.90 ungulates/week, 95% CI = 0.65–1.16).

When comparing seasonal (summer vs winter) effects across demographic classes, we found significant differences in ungulate kill ($F_{5,11} = 2.934$, $P = 0.064$) and ungulate consumption ($F_{5,11} = 2.916$, $P = 0.065$) rates; however, biomass consumed per week did not differ ($F_{5,11} = 0.870$, $P = 0.531$; Figure 2). Our results were limited to one

adult female without kittens for the summer season; this female was only collared for June and July (time of highest ungulate kill rate). Excluding this female, ungulate kill rate ($F_{5,10} = 0.881$, $P = 0.506$) and ungulate consumption rate ($F_{5,10} = 0.919$, $P = 0.487$) were similar for seasonal demographic classes.

DISCUSSION

Our study represents the first research conducted on North Dakota's recently recolonized population of mountain lions in the Little Missouri Badlands. This population occurs on the eastern edge of mountain lion range (Larue et al. 2012) where environmental conditions (e.g., habitat, prey guilds, anthropogenic influences, land use) vary from western populations and where mountain lions represent the lone large carnivore. Mountain lions persist within a relatively small region of North Dakota where breeding range is estimated at 2,671 km² (Tucker 2013), less than one third the area of another recently studied Midwestern population (8,400 km² Black Hills, South Dakota; Fecske 2003). Estimated population size within the region also was relatively low (Tucker 2013); thus, our sample of radio-collared individuals represents a considerable proportion of North Dakota's resident mountain lion population.

We documented higher overall ungulate kill rates for mountain lions in our study area compared to recent studies using similar methodology (Knopff et al. 2010, Smith et al. In Review). Variation in reported ungulate kill rates between our study and Knopff et al. (2010) was likely due to differences in body size of available ungulate prey between study areas. Deer (76.9%) were the primary ungulate prey for mountain lions in North Dakota. Although bison were available within TRNP, elk were the only large ungulate prey consumed by mountain lions and they accounted for a minimal portion of the annual

diet (2.1% males; 0% ad females). Additionally, calves comprised 100% of elk killed by mountain lions in our study. In contrast, Knopff et al. (2010) found that large ungulates (elk, moose [*Alces americanus*], feral horse [*Equus caballus*]) played a much greater role in mountain lion diets in Alberta (48.4% ad males; 8.6% ad females). Similar to Knopff et al. (2010), Smith et al. (In Review) found high proportions of large ungulates in adult male mountain lion diets (20.1%). Additionally, Smith et al. (In Review) saw much greater reliance on scavenged prey items (17.3%) compared to the North Dakota Badlands (6.7%), allowing mountain lions to persist in the Black Hills without making as many kills. Use of larger prey items and higher scavenge rates are likely drivers of a lower ungulate kill rate for mountain lions documented in the Black Hills and Alberta. Additionally, both Knopff et al. (2010) and Smith et al. (In Review) found subadult females to have the lowest kill rates of any demographic group and family groups to have the highest. Our study did not include any subadult females and had a high proportion of family groups, which likely contributed to our higher estimates of overall ungulate kill rate.

Though our seasonal comparisons may be influenced by variation among individuals due to the small number of radio collared mountain lions ($n = 2$) that maintained demographic class through both seasons, we did see similar dietary shifts in both males and females. Mountain lion diets contained much higher proportions of juvenile ungulates (60.7%) during the fawning season than the remainder of the year, suggesting selection for these ungulates during this time (Knopff et al. 2010). The ungulate birth pulse represents a time of high ungulate densities, and high vulnerability for neonates, resulting in an increased encounter rate and increased risk of predation at

each encounter (Lingle et al. 2008). This shift to juveniles after the ungulate birth pulse resulted in a substantial increase in ungulate kill rate (1.61 times greater in June–August). Such shifts also have been found in previous studies (Knopff et al. 2010, Smith et al. In Review) and should be considered when evaluating potential impacts of mountain lion predation on ungulate populations. Additionally, we found considerable increases in nonungulate consumption during summer by males and females, which was contrary to findings of Knopff et al. (2010). Beaver and porcupine were the primary nonungulate prey items in mountain lion diets in North Dakota. Increase in beaver consumption was likely attributed to their increased availability in summer after ice out. Increase in porcupine consumption in summer was mainly due to the propensity of one young adult male to kill porcupines, which accounted for 75% of porcupines killed in summer, and 67% of all porcupines killed. We did not find significant seasonal differences in biomass consumed; this may be partially a result of our biomass estimates for scavenge sites. Our assessment of scavenged biomass likely represents an overestimation due to uncertainty in true consumption and thus, potentially inflated estimates of total biomass consumed in winter when scavenge events were more prevalent.

Due to small sample size, we separated our mountain lion sample into 3 groups: males (1 subadult, 5 adults), independent females (3 adults), and females with kittens (3 adults), unlike the 6 demographic groups compared by Knopff et al. (2010) and Smith et al. (In Review). Our findings are similar to those of previous studies (Anderson and Lindzey 2003, Knopff et al. 2010, Smith et al. In Review), with family groups having the highest ungulate kill and consumption rates, followed by independent females, and males. Higher energetic needs of family groups (Laundré 2005) likely explain their higher

feeding rates; variation within our winter family group class was likely due to differences in age of kittens not accounted for in our grouping. Intuitively, one might expect male mountain lions to have higher kill rates than independent females due to their larger size (Laundré 2005); however, tendency of males to take more larger bodied ungulate prey in winter ($\bar{x} = 59.11$ kg) than females ($\bar{x} = 47.67$ kg) likely explains the similar kill rates we observed.

Estimated overall scavenge rates (6.7%) in our study area were comparable to those for mountain lions in Alberta, Canada (5.8%; Knopff et al. 2010), but much lower than rates reported for Black Hills, South Dakota (17.3%; Smith et al. In Review), where anthropogenic influences were much greater. Sources of scavenged prey included road-kill, hunter-wounding loss, winter-kill, and mountain lions sharing prey items. Although scavenging occurred throughout the year, higher rates were observed in winter (11.9%) than summer 3.7%, consistent with patterns found in previous studies (Bauer et al. 2005, Knopff et al. 2010, Smith et al. In Review). Colder winter conditions likely influenced scavenge rates by slowing or halting decomposition of potential prey items, which allowed greater time for mountain lions to encounter them. Additionally, higher energetic needs in winter for thermoregulation may lead to an increased tendency of mountain lions to conserve energy by scavenging items they would normally ignore in summer.

There are several potential biases to consider that may have influenced scavenging rates. If there was no sufficient evidence at a site to suggest otherwise, our default classification was probable mountain lion kill. Complete consumption of a carcass prior to investigation may have resulted in misclassification of scavenged prey

items as kills. Additionally, prey killed by unmarked mountain lions and subsequently scavenged by marked individuals, or the sharing of prey items by mountain lions, may have caused similar misclassifications. Additional information from our bait sites indicates that mountain lions exhibiting scavenging behavior may not stay at a scavenge site long enough for the formation of a GPS cluster, resulting in an underestimation of the influence of scavenging on mountain lion diets. Number of individuals that fed at our bait sites, but were not captured, indicated that scavenging may occur more in this system than demonstrated by our marked individuals. Conversely, our method of capture may have biased scavenge rates high. By capturing mountain lions using bait sites, we may have potentially selected mountain lions with an increased propensity toward scavenging.

Our assessment of small prey consumed also may represent an underestimation as mountain lions would likely exhibit shorter handling times with these items, which could result in clusters not generated at these sites. Increasing the number of locations collected per day from GPS collars may allow researchers to identify these small prey items more readily; however, this would substantially increase intensity of field work and decrease efficiency by incorporating more no-prey sites that would have to be investigated. Additionally, small prey items may not be found at clusters due to complete consumption of prey by mountain lions.

High proportions of private land within Midwestern mountain lion populations provide an additional challenge for researchers. Although our study area was focused mainly within the Little Missouri National Grassland, eastern portions were comprised almost entirely of private lands (Figure 1). Cooperation with private landowners was generally amicable; however, we were denied access to a few large tracts resulting in a

considerable number of non-investigated clusters. Use of logistic regression modeling allowed us to predict potential predation for clusters we were not able to investigate. Despite having to predict feeding events for a large number of clusters (51.4%), our model estimated that 11.6% of these clusters contained prey items, representing 17.3% of the total number of carcasses (investigated + predicted) used to calculate feeding rates. To verify the efficacy of our predictions, we applied Smith et al.'s (In Review) top logistic regression model for predicting mountain lion predation events in the Black Hills, South Dakota to our non-investigated clusters. Using the provided beta values and prediction cutoff value, this model predicted similar results (9.5% predicted to contain prey items) for our non-investigated clusters. We believe that the low proportion of predicted feeding events at non-investigated clusters was likely due to the behavior of mountain lions within areas where we were denied access and not from model bias. For example, the Killdeer Mountain region was connected to the nearest Badlands habitat by a single privately owned 5-km long drainage surrounded by agricultural lands and oil/gas development. We routinely saw individuals using this drainage as a corridor between the two habitats; however, rarely did they stay within it for extended time periods. Smaller clusters within this corridor, and other similar travel-ways across "non-traditional" habitats (e.g., short-grass prairie), were likely generated as a result of movement patterns, not feeding events. This behavior resulted in a much larger proportion of non-investigated clusters having a low number of cluster hours compared to our investigated clusters. The average duration (first coordinate minus last coordinate) for all non-investigated clusters was 25.32 hours (SE = 1.68), 38.75 hours (SE = 1.89) for investigated sites, and 53.33 hours (SE = 2.48) for known consumption sites. The shorter

period of time spent at non-investigated clusters is a probable explanation for the lower proportion of predicted feeding events generated by our model for these sites.

Additionally, non-investigated clusters had a much lower number of night time locations (1.87 night locations/cluster) when compared to investigated clusters (5.09 night locations/cluster); investigated sites with prey items present contained an average of 7.20 night locations/cluster. This lower number of night locations is likely due to mountain lions creating clusters at day bed locations while traversing “non-traditional” habitats; Ruth et al. (2010) found that the proportion of clusters containing bed sites or mountain lion sign, but no prey items, was highest when the clusters were generated between 0800–1700 hrs. Over- or underestimation of prey consumption by our model has the potential to alter our estimated feeding rates; however, we believe that they approximate true rates for mountain lions inhabiting the Badlands Region of North Dakota.

Use of GPS collars allows for increased length of monitoring periods, providing improved precision in predation estimates (Knopff et al. 2009). Additionally, real-time GPS collars have allowed researchers to reduce time between cluster formation and investigation, leading to easier identification of prey remains and cause of death (Anderson and Lindzey 2003, Knopff et al. 2009, Smith et al. In Review). Although care should be taken to ensure mountain lions are not prematurely displaced from carcasses, potentially altering feeding habits (Knopff et al. 2010, Miller et al. 2013), we do not suspect that these displacements would introduce excessive bias; we routinely found mountain lions returning to bait sites where they had been captured, given that edible bait was still present at the site.

Application of our feeding rates to other study areas should be performed with caution. Variation in ecological conditions (e.g., predator and prey guilds, mountain lion population structure, habitat) has the potential to alter predation characteristics considerably. A larger sample of mountain lions would increase the precision of our estimates and more data are needed to differentiate potential differences in predation rates for mountain lions between seasons and among demographic groups. Nevertheless, our study demonstrates the efficacy of GPS collars in estimating predation rates and provides insight into the feeding ecology of mountain lions in a recently recolonized, previously unstudied, Midwestern population. GPS collar technology coupled with modern modeling techniques provides researchers a method of quantifying mountain lion feeding events in a landscape that does not allow for investigation of all potential feeding sites. Use of these techniques will prove valuable as mountain lions continue range expansion into regions with high proportions of private lands (e.g., Midwestern states).

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FIGURE 1.—Our study area was focused within the Little Missouri Badlands of western North Dakota from 2012–2013.

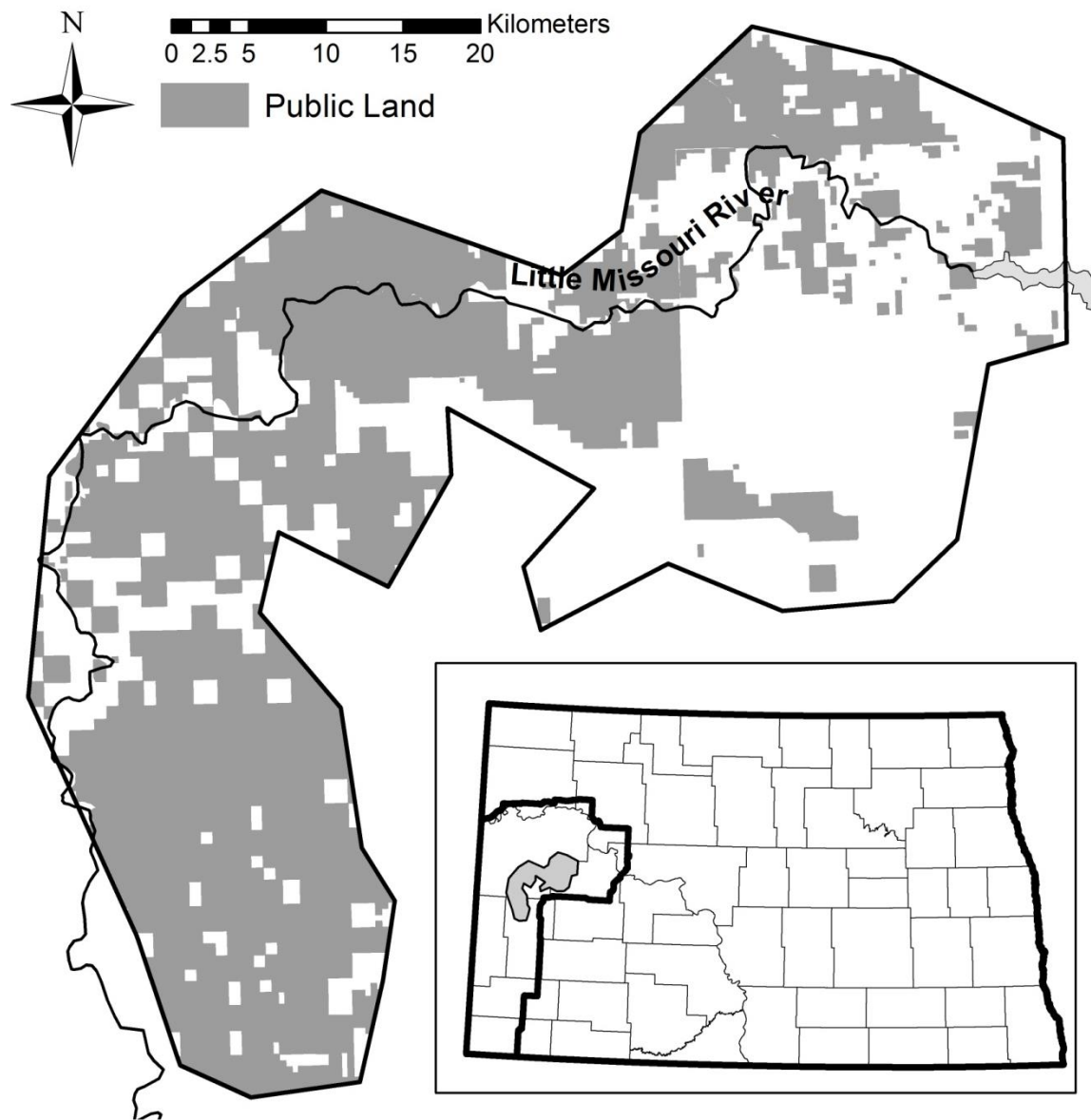
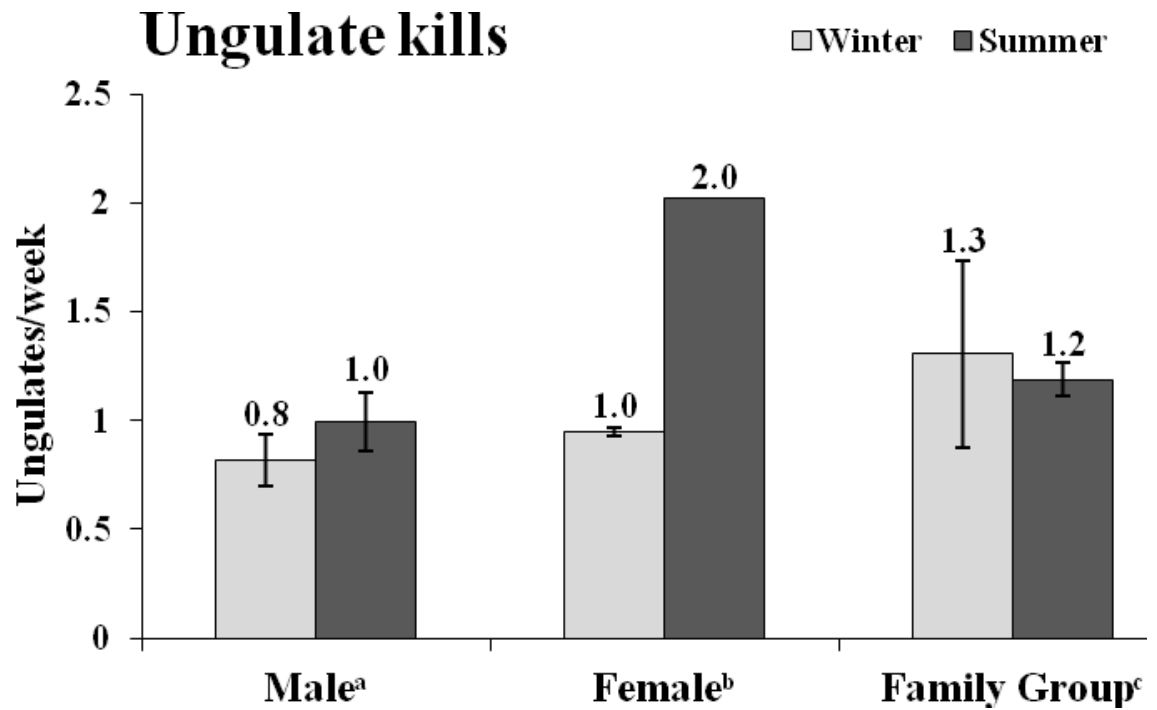
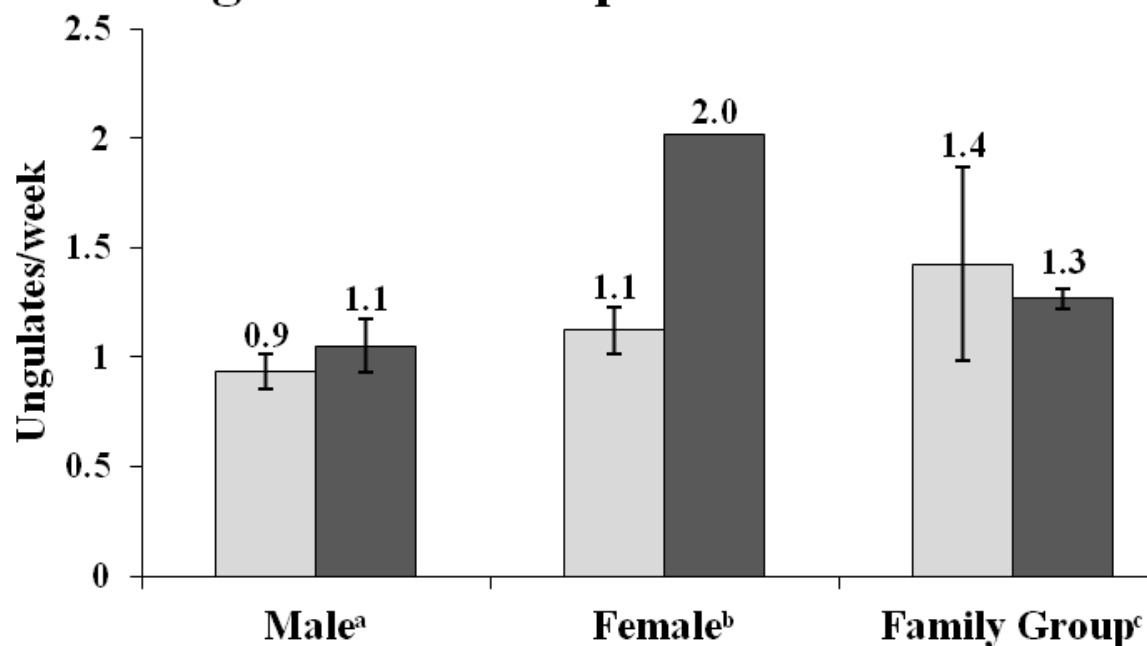


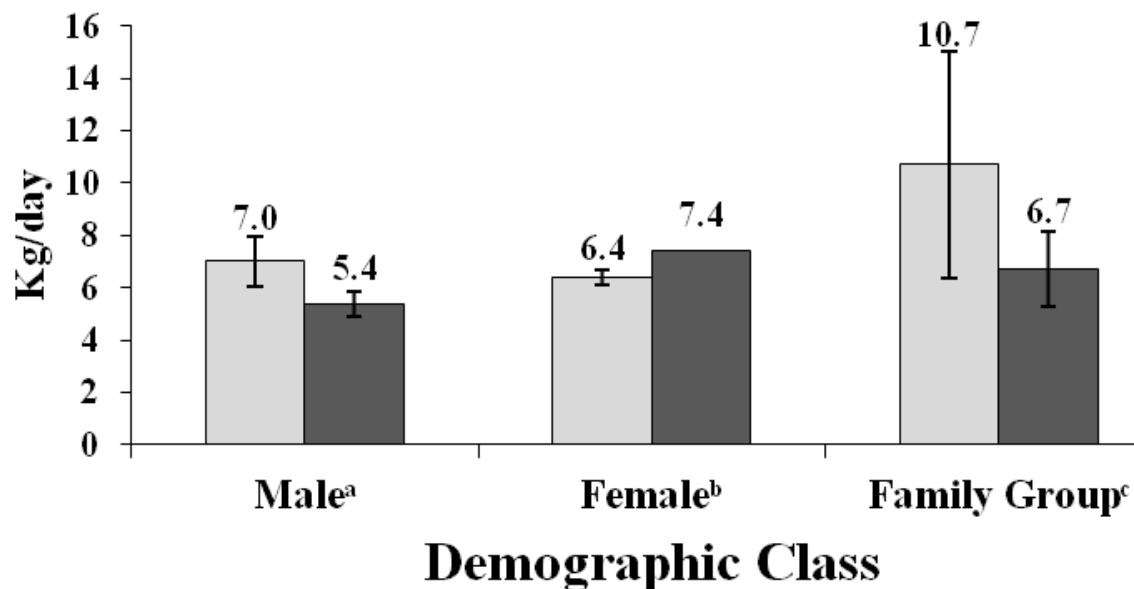
FIGURE 2.— Mountain lion ungulate kill rates, ungulate consumption rates, and total biomass consumed and associated standard errors for each demographic class (male, female, family group [female with dependent young]) and season in western North Dakota, USA July 2012–July 2013.



Ungulate consumptions



Total Biomass



^a Male—winter, $n = 4$; summer, $n = 5$

^b Female—winter, $n = 2$; summer, $n = 1$

^c Family group—winter, $n = 2$; summer, $n = 3$

TABLE 1.—Ungulate weight estimates (kg) used to calculate biomass rates (kg/day) for mountain lions (*Puma concolor*) in western North Dakota, USA, July 2012–July 2013.

Age and sex class	Species		
	Deer	Elk	Bighorn Sheep
Ad M	75 ^a	317 ^a	104 ^b
Ad F	61 ^a	225 ^a	70 ^b
Yearling (12–24 months)	50 ^c	186 ^c	58 ^c
YOY ^d (6–12 months)	32 ^c	118 ^c	37 ^c
YOY (3–6 months)	18 ^c	65 ^c	20 ^c
YOY (0–3 months)	8 ^c	29 ^c	9 ^c

^a Weight estimates obtained from Jensen (2000).

^b Weight estimates obtained from South Dakota State University, unpublished data.

^c We derived median weight estimates for non-adult age classes using a von Bertalanffy growth equation of the form $M(t) = A[1 - 1/3e^{-K(t-I)}]$, where $M(t)$ = mass (kg) at age t , A = max. wt (we used weight of adult female), K = growth rate (we used 0.0042), and I = age at inflection point (we used 140 days).

^d YOY = young of the year.

TABLE 2.—Seasonal composition of prey^a items ($n = 292$) by frequency in the diet of 4 adult female, 1 subadult male (transitioned to adult mid-study), and 5 adult male mountain lions (*Puma concolor*) in western North Dakota, July 2012 – July 2013.

Prey	F (%) ($n = 4$)		M (%) ($n = 5$)	
	Summer ($n = 65$)	Winter ($n = 39$)	Summer ($n = 122$)	Winter ($n = 66$)
Beaver	4.62	0.00	12.00	2.99
Bighorn sheep	4.62	4.76	1.60	1.49
Bovine	0.00	0.00	2.40	0.00
Cottontail	1.54	0.00	0.80	0.00
Coyote	4.62	0.00	1.60	0.00
Deer spp.	15.38	2.38	24.00	0.00
Elk	0.00	0.00	2.40	1.49
Mountain lion	0.00	0.00	0.00	1.49
Mule deer	55.38	83.33	37.60	65.67
Porcupine	3.08	2.38	8.00	2.99
Raccoon	3.08	2.38	0.00	0.00
Turkey	4.62	0.00	0.00	0.00
White-tailed deer	3.08	4.76	9.60	16.42
Bait	0.00	0.00	0.00	7.46
Prey group				
Nonungulate	21.54	4.76	24.80	7.46
Ungulate	78.46	95.24	75.20	92.54
Scavenge	3.08	11.90	4.00	11.94

^aIncludes mountain lion killed and scavenged prey

TABLE 3.—The top 10 multivariate logistic regression models for predicting consumption of prey items ≥ 4 kg by mountain lions (*Puma concolor*) at 506 GPS location clusters in western North Dakota, July 2012 – July 2013.

Model Description	<i>K</i>	AIC	Δ AIC	AIC weight	Evidence ratio
Hours ^a + Avg Dist ^b + Night Prop ^c + Season + Fidelity ^d	5	426.166	0.000	0.561	1.000
Hours + Avg Dist + Night Prop + Fidelity	4	428.504	2.337	0.174	0.310
Points ^e + Avg Dist + Night Prop + Season + Fidelity	5	430.572	4.406	0.062	0.111
Avg Dist + Night Points ^f + Fidelity	3	431.620	5.454	0.037	0.066
Avg Dist + Night Points + Night Prop + Season + Fidelity	5	431.849	5.683	0.033	0.059
Points + Avg Dist + Night Prop + Fidelity	4	432.641	6.475	0.022	0.039
Hours + Night Prop + Fidelity	3	432.727	6.561	0.021	0.037
Night Prop + Hours + Fidelity	3	432.727	6.561	0.021	0.037
Avg Dist + Night Points + Night Prop + Fidelity	4	432.867	6.701	0.020	0.036
Night Prop + Points + Fidelity	3	436.675	10.509	0.003	0.005

^a Hours = total number hours between the first and last location in cluster.

^b Avg Dist = average distance that each location in cluster was from cluster centroid.

^c Night Prop = total number of locations obtained between 1800–0600 hrs in cluster divided by total number of locations in cluster.

^d Fidelity = number of locations in cluster minus number of locations away from cluster during cluster duration.

^e Points = total number of locations within the cluster.

^f Night Points = total number of locations within the cluster obtained between 1800 and 0600 hrs.

TABLE 4.—Beta coefficients from the top multivariate logistic regression model for predicting mountain lion (*Puma concolor*) feeding sites from non-feeding sites, and predicting large prey ($\geq 34\text{kg}$) or small prey ($< 34\text{kg}$) feeding sites from 506 GPS location clusters in western North Dakota, July 2012 – July 2013.

Pr (prey, no prey)				Pr (large prey, small prey)			
Covariate	Coefficient	SE	P-value	Covariate	Coefficient	SE	P-value
Constant (β_0)	-4.367	0.586	<0.001	Constant (β_0)	-1.414	0.512	0.006
Hours ^a	0.061	0.007	<0.001	Days ^f	1.173	0.181	<0.001
Avg Dist ^b	-0.013	0.005	0.009	Season	-1.928	0.380	<0.001
Night Prop ^c	3.268	0.490	<0.001	Fidelity	0.040	0.019	0.033
Season ^d	0.638	0.310	0.039				
Fidelity ^e	0.256	0.032	<0.001				

^a Hours = total number hours between the first and last location in cluster.

^b Avg Dist = average distance that each location in cluster was from cluster centroid.

^c Night Prop = total number of locations obtained between 1800–0600 hrs in cluster divided by total number of locations in cluster.

^d Season = season (summer = 15 May–15 November; winter = 16 November–14 May) in which cluster was generated.

^e Fidelity = number of locations in cluster minus number of locations away from cluster during cluster duration.

^f Days = number of 24-hr periods in which ≥ 1 location was collected within cluster.

TABLE 5.—The top 10 multivariate logistic regression models for predicting consumption of large ($\geq 34\text{kg}$) or small ($< 34\text{kg}$) prey items by mountain lions (*Puma concolor*) at 506 GPS location clusters in western North Dakota, July 2012 – July 2013.

Model Description	K	AIC	ΔAIC	AIC weight	Evidence ratio
Days ^a + Season + Fidelity ^b	3	241.958	0.000	0.609	1.000
Days + Season	2	244.692	2.733	0.155	0.255
Days + Radius ^c + Night Prop ^d + Season + Fidelity	5	245.304	3.346	0.114	0.188
Days + Avg Dist ^e + Night Prop + Season + Fidelity	5	245.449	3.490	0.106	0.175
Hours ^f + Avg Dist + Night Prop + Season + Fidelity	5	250.145	8.186	0.010	0.017
Points ^g + Season	2	251.758	9.800	0.005	0.007
Points + Avg Dist + Night Prop + Season + Fidelity	5	256.004	14.046	0.001	0.001
Avg Dist + Night Points + Night Prop + Season + Fidelity	5	258.127	16.169	0.000	0.000
Radius + Night Points + Night Prop + Season + Fidelity	5	258.163	16.205	0.000	0.000
Hours + Season	2	267.205	25.246	0.000	0.000

^a Days = number of 24-hr periods in which ≥ 1 location was collected within cluster.

^b Fidelity = number of locations in cluster minus number of locations away from cluster during cluster duration.

^c Radius = difference between cluster centroid and the furthest cluster location.

^d Night Prop = total number of locations obtained between 1800–0600 hrs in cluster divided by total number of locations in cluster.

^e Avg Dist = average distance that each location in cluster was from cluster centroid.

^f Hours = total number hours between the first and last location in cluster.

^g Points = total number of locations within the cluster.

APPENDIX A

**SUMMARY OF NORTH DAKOTA GAME AND FISH
DEPARTMENT MOUNTAIN LION (*Puma concolor*) NECROPSY
REPORTS, 1991-2013.**

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2014

Table A–1. Carnivore parvovirus test results (CPV; $n = 23$) from mountain lions (*Puma concolor*) necropsied by North Dakota Game and Fish Department (NDGFD). Carcasses were obtained from hunter harvest, incidental snaring/trapping, depredation removal, vehicle collision, and illegal take. Tissue samples were tested by Cornell University (Baker Institute for Animal Health, Ithaca, NY, USA). Overall prevalence of CPV was 69.6%, divided between two strains, CPV–2b (56.5%) and CPV–2c (13.0%).

Mountain Lion ID	Sex	County	Mortality Date	Age (yrs)	Sample/s Tested	Test Result
75	F	McKenzie	8/9/2011	2	spleen, tongue	CPV-2b
78	F	McKenzie	9/10/2011	1	spleen	CPV-2b
81	F	Dunn	10/14/2011	6	spleen, tongue	negative
82	F	McKenzie	10/27/2011	4	spleen, tongue	negative
83	F	McKenzie	11/5/2011	3	spleen, tongue	CPV-2b
84 ^a	M	Emmons	11/6/2011	2	spleen	CPV-2b
85	F	McKenzie	11/8/2011	6	spleen, tongue	negative
86	F	Dunn	11/12/2011	3	spleen, tongue	CPV-2b
88	F	Dunn	11/15/2011	2	spleen, tongue	negative
201	F	Dunn	11/26/2011	0	spleen	CPV-2b
90	M	McKenzie	12/5/2011	4	spleen, tongue	CPV-2b
91	F	McKenzie	12/5/2011	2	spleen, tongue	negative
92	F	McKenzie	12/5/2011	3	spleen, tongue	CPV-2b
93	F	Dunn	12/17/2011	3	spleen, tongue	CPV-2c
94	F	McKenzie	12/21/2011	0	spleen, tongue	CPV-2b
95	F	Dunn	12/31/2011	2	spleen, tongue	negative
96	M	Dunn	1/14/2012	2	spleen, tongue	CPV-2b
97	F	McKenzie	1/18/2012	4	spleen, tongue	negative
98	F	McKenzie	1/19/2012	1	spleen, tongue	CPV-2b
202 ^a	M	Mercer	2/6/2012	3	spleen, tongue	CPV-2c
203	M	McKenzie	2/11/2012	1	spleen, tongue	CPV-2b
101	M	McKenzie	3/30/2012	1	spleen, tongue	CPV-2b
205	F	McKenzie	8/28/2012	2	spleen, tongue	CPV-2c

^aCollected outside of NDGFD mountain lion hunt Zone 1.

Table A–2. Gastrointestinal (GI) contents of mountain lions (*Puma concolor*) necropsied by North Dakota Game and Fish Department (NDGFD). Carcasses ($n = 84$) were obtained from hunter harvest, incidental snaring/trapping, depredation removal, vehicle collision, and illegal take within NDGFD mountain lion hunt Zone 1.

Mountain Lion ID	Sex	County	Mortality Date	Age (yrs)	GI Tract Contents
1277	F	Golden Valley	1/18/1991	0	porcupine
6	F	McKenzie	7/9/2006	1	porcupine
7	F	McKenzie	9/16/2006	0	empty
17	F	McKenzie	5/27/2007	0	porcupine
21	F	Dunn	9/16/2007	1	empty
27	M	Billings	12/17/2007	4	deer
29	F	McKenzie	2/13/2008	0	vegetation
31	F	Dunn	7/29/2008	0	porcupine
32	F	McKenzie	9/17/2008	4	empty
33	M	McKenzie	9/27/2008	1	fox squirrel
35	F	McKenzie	11/8/2008	1	vegetation
36	M	McKenzie	11/10/2008	1	empty
37	M	McKenzie	11/15/2008	0	deer
38	M	McKenzie	11/15/2008	0	deer
41	F	McKenzie	9/26/2009	3	empty
43	M	McKenzie	10/12/2009	2	empty
45	F	McKenzie	10/31/2009	4	deer, turkey
48	F	McKenzie	12/5/2009	3	empty
49	F	McKenzie	12/11/2009	2	empty
50	M	Dunn	12/29/2009	1	empty
51	M	Dunn	12/30/2009	4	empty
52	M	McKenzie	6/6/2010	4	porcupine
53	F	Dunn	9/27/2010	4	empty
56	M	Billings	11/6/2010	1	porcupine
57	F	Dunn	11/7/2010	2	empty
58	M	McKenzie	11/10/2010	0	porcupine
59	F	McKenzie	11/10/2010	0	porcupine
61	M	Dunn	11/12/2010	3	porcupine
66	F	Dunn	1/14/2011	4	deer
71	M	Dunn	2/27/2011	3	empty
72	M	Dunn	3/7/2011	0	deer
74	M	Dunn	4/22/2011	2	empty
75	F	McKenzie	8/9/2011	2	empty

Table A-2 cont.

76	F	McKenzie	9/6/2011	2	deer
77	F	McKenzie	9/10/2011	3	empty
80	M	Dunn	9/24/2011	5	deer
81	F	Dunn	10/14/2011	6	empty
82	F	McKenzie	10/27/2011	4	empty
83	F	McKenzie	11/5/2011	3	empty
85	F	McKenzie	11/8/2011	6	empty
86	F	Dunn	11/12/2011	3	porcupine
88	F	Dunn	11/15/2011	2	deer, vegetation
201	F	Dunn	11/26/2011	0	empty
90	M	McKenzie	12/5/2011	4	empty
91	F	McKenzie	12/5/2011	2	deer
92	F	McKenzie	12/5/2011	3	empty
93	F	Dunn	12/17/2011	3	empty
94	F	McKenzie	12/21/2011	0	domestic cat
95	F	Dunn	12/31/2011	2	deer
96	M	Dunn	1/14/2012	2	empty
97	F	McKenzie	1/18/2012	4	empty
98	F	McKenzie	1/19/2012	1	empty
200	F	Dunn	1/20/2012	1	deer
203	M	McKenzie	2/11/2012	1	porcupine
204	M	Dunn	2/28/2012	5	porcupine
205	F	McKenzie	8/28/2012	2	domestic sheep
206	F	Dunn	9/25/2012	2	domestic goat
207	M	Billings	11/18/2012	3	deer, beaver
208 (MT-M3)	M	McKenzie	12/4/2012	4	deer
209	M	McKenzie	12/8/2012	1	deer
211	M	McKenzie	12/8/2012	3	empty
210	F	Billings	12/9/2012	0	empty
212	F	McKenzie	12/11/2012	5	deer
215	F	McKenzie	12/12/2012	-	empty
106	M	McKenzie	12/13/2012	6	deer
109	F	McKenzie	12/14/2012	1	deer
213	F	McKenzie	12/14/2012	3	empty
214	F	Dunn	12/18/2012	2	chicken
216	F	Dunn	12/28/2012	4	porcupine
217	M	Dunn	12/30/2012	2	empty
218	F	McKenzie	12/31/2012	6	empty
223	F	McKenzie	6/26/2013	2	deer
114	M	Billings	7/8/2013	5	domestic cattle
224 (MT-M6)	M	Billings	9/28/2013	2	empty
226	M	Dunn	11/2/2013	1	empty

Table A-2 cont.

228	M	McKenzie	11/8/2013	3	empty
107	M	Billings	11/16/2013	2	empty
229	F	Billings	11/21/2013	1	empty
230	F	McKenzie	11/27/2013	4	deer
231	M	Slope	12/8/2013	2	deer
112	F	McKenzie	12/14/2013	3	empty
233	F	Dunn	12/14/2013	1	porcupine
234	M	Billings	12/14/2013	6	deer
235	F	Billings	12/14/2013	1	deer

Table A-3. Placental scar counts from female mountain lions (*Puma concolor*) ≥ 2 yrs necropsied by North Dakota Game and Fish Department (NDGFD). Carcasses ($n = 63$) were obtained from hunter harvest, incidental snaring/trapping, depredation removal, vehicle collision, and illegal take within NDGFD mountain lion hunt Zone 1.

Mountain Lion ID	County	Mortality Date	Age (yrs)	Placental Scar Count
1277	Golden Valley	1/18/1991	0	0
1	McKenzie	11/16/2005	2.5	2
6	McKenzie	7/9/2006	1	0
7	McKenzie	9/16/2006	0	0
15	McKenzie	2/18/2007	14	4
17	McKenzie	5/27/2007	0	0
19	McKenzie	9/1/2007	4	3
21	Dunn	9/16/2007	1	0
22	Dunn	9/17/2007	1	0
23	McKenzie	10/30/2007	1	0
25	McKenzie	12/12/2007	1	0
26	McKenzie	12/12/2007	1	4
29	McKenzie	2/13/2008	0	0
31	Dunn	7/29/2008	0	0
32	McKenzie	9/17/2008	4	3
34	McKenzie	10/25/2008	1	0
35	McKenzie	11/8/2008	1	2
39	Dunn	2/16/2009	0	0
41	McKenzie	9/26/2009	3	2
44	McKenzie	10/23/2009	3	1
45	McKenzie	10/31/2009	4	2
46	McKenzie	11/19/2009	4	3
48	McKenzie	12/5/2009	3	0
49	McKenzie	12/11/2009	2	0
53	Dunn	9/27/2010	4	4
57	Dunn	11/7/2010	2	0
62	McKenzie	11/12/2010	10	3
75	McKenzie	8/9/2011	2	0
76	McKenzie	9/6/2011	2	0
78	McKenzie	9/10/2011	1	0
77	McKenzie	9/10/2011	3	3
79	Dunn	9/17/2011	3	3
81	Dunn	10/14/2011	6	4

Table A-3 cont.

82	McKenzie	10/27/2011	4	4
83	McKenzie	11/5/2011	3	3
85	McKenzie	11/8/2011	6	2
86	Dunn	11/12/2011	3	5
87	McKenzie	11/13/2011	8	4
201	Dunn	11/26/2011	0	0
91	McKenzie	12/5/2011	2	1
92	McKenzie	12/5/2011	3	3
93	Dunn	12/17/2011	3	1
94	McKenzie	12/21/2011	0	0
95	Dunn	12/31/2011	2	2
99	Dunn	1/16/2012	3	5
97	McKenzie	1/18/2012	4	3
98	McKenzie	1/19/2012	1	0
200	Dunn	1/20/2012	1	0
205	McKenzie	8/28/2012	2	0
206	Dunn	9/25/2012	2	3
210	Billings	12/9/2012	0	0
212	McKenzie	12/11/2012	5	3
109	McKenzie	12/14/2012	1	0
213	McKenzie	12/14/2012	3	0
214	Dunn	12/18/2012	2	3
216	Dunn	12/28/2012	4	3
218	McKenzie	12/31/2012	6	4
223	McKenzie	6/26/2013	2	1
229	Billings	11/21/2013	1	0
230	McKenzie	11/27/2013	4	3
233	Dunn	12/14/2013	1	3
235	Billings	12/14/2013	1	2
112	McKenzie	12/14/2013	3	4