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2 authors:

Brett P. Wiedmann
North Dakota State Water Commission

Vernon C. Bleich
University of Nevada, Reno

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Original Article

Demographic Responses of Bighorn Sheep to Recreational Activities: A Trial of a Trail

BRETT P. WIEDMANN,[1] *North Dakota Game and Fish Department, 225 30th Avenue SW, Dickinson, ND 58601, USA*
VERNON C. BLEICH, *Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, USA*

ABSTRACT Long-term effects of anthropogenic disturbance to wildlife, and whether such effects have population-level consequences, often are difficult to determine. In 1996, a recreational hiking trail (Maah Daah Hey Trail [Trail]) was constructed by the U.S. Forest Service through 4 geographic areas, each occupied by a distinct sub-population of bighorn sheep (*Ovis canadensis*), in western North Dakota, USA. From 2001 to 2012, we monitored distribution, recruitment rates, and abundance of female bighorn sheep in the sub-populations to investigate responses to activities associated with the Trail, and whether demographic consequences occurred. Female bighorn sheep at Sully Creek were displaced from, and eventually abandoned, lambing habitat subjected to intensive recreational use that was erratic and unpredictable. Consequently, females inhabiting Sully Creek had lower fidelity to lambing areas than did other sub-populations, all of which realized 100% fidelity. Further, females inhabiting Sully Creek achieved lower recruitment of young, exhibited a substantial downward trend in recruitment rate, and a decline in abundance of females compared with the other sub-populations also exposed to the Trail, but where perturbation was less severe and human activities were consistent, predictable, and spatial separation existed between recreationists and lambing habitat. Metapopulations of bighorn sheep occurring in fragmented habitat having minimal vertical relief may be especially susceptible to sources of disturbance, which should be a consideration when recreational facilities are developed.

KEY WORDS bighorn sheep, disturbance, lambing area, North Dakota, *Ovis canadensis*, recreation, recruitment, trails.

Two fundamental questions are related directly to the responses of wildlife to environmental disturbance (Moorcroft 2012): how is the spatial distribution of animals affected; and, does (or did) the disturbance result in effects that ultimately had demographic consequences for the perturbed population? Responses by wildlife are sometimes not immediately evident (Schoenecker and Krausman 2002), but disturbances over extended periods can cause animals to alter patterns of habitat use or avoid disturbed areas. As a result, population-level effects of disturbance are difficult to document because of inter-annual variation in environmental factors (Wehausen et al. 1987, Wehausen 2005) or combinations thereof (Pierce et al. 2012), with resultant influences on variability in demographic parameters (e.g., recruitment rate; Oehler et al. 2005). Further confounding the detection of population-level responses to disturbance are the prior experiences of ungulates with human activities (Stankowich 2008).

Long-term demographic investigations over a continuum of conditions are necessary to fully understand the responses of ungulate populations to multiple factors (Bleich et al. 2006; Monteith et al. 2011, 2014; Pierce et al. 2012). Although such studies are expensive and difficult to implement (Beale 2007), effects of disturbance or cumulative perturbations have implications for the fitness of individuals (Ciuti et al. 2012), with resultant population-level consequences (Stockwell et al. 1991, Bleich et al. 1994, Côté 1996). For example, animals with habitat of similar quality nearby may be able to avoid disturbances because they have alternate sites to occupy (Longshore et al. 2013), but such is not always the case. Indeed, if animals abandon habitat in response to disturbance and move to areas that are less suitable in terms of forage or cover, it is likely that individual fitness will suffer, which could translate into population-level impacts. Gill et al. (2001) emphasized that meaningful studies must address behavioral changes in response to disturbance in the context of demographic changes, and such changes are of primary concern in terms of their implications for conservation (Knight and Gutzwiller 1995) and can serve to inform future management decisions (Yoccoz et al. 2001). Hence, an understanding of how wildlife responds to anthropogenic disturbance is an important consideration (Dzialak et al. 2011).

The effects of disturbance are likely to be exacerbated for animals living in heterogeneous environments, as do North American wild sheep (*Ovis canadensis* and *O. dalli*), where critically important resources are limited and widely distributed across the landscape (Bleich et al. 1990, 1994). The long-term effects of disturbance may be especially

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[1]*E-mail: bwiedmann@nd.gov*

onerous because wild sheep are habitat specialists, almost always give birth to a single offspring, and recruitment rates typically are low (Shackleton 1985, Bowyer and Leslie 1992, Bowyer et al. 2000, Krausman and Bowyer 2003).

Bighorn sheep have a narrow habitat niche (Geist 1971*a*; Hansen 1980; Bleich et al. 1990, 1997) and may be more vulnerable to anthropogenic disturbances than habitat generalists such as mule deer (*Odocoileus hemionus*) or North American elk (*Cervus elaphus;* Johnson 1983, Singer et al. 2000). Responses of bighorn sheep are influenced strongly, however, by the consistency, predictability, and level of threat associated with each source of disturbance (Jansen et al. 2006, 2007, 2009; Bleich et al. 2009), rather than the mere presence of humans or other perturbations. Nevertheless, the severity of a response may not diminish after successive events perceived to be especially threatening (Bleich et al. 1994) but, instead, may increase (MacArthur et al. 1982).

Female bighorn sheep have high fidelity to traditional birthing and rearing areas (Geist 1971*a*, Becker et al. 1978), and such areas often are selected by parturient females over those with higher quality forage (Berger 1991, Bleich et al. 1997) because females and precocial lambs use escape terrain (i.e., steep, rugged terrain with high visibility often used as lambing habitat) to evade predators (Geist 1971*a*, Festa-Bianchet 1988, Bleich 1999). Lambing range, therefore, plays importantly in the survival of neonates (Singer et al. 1997). In the absence of nutritional limits, Holl (1982) reported that the quantity of escape terrain is a predictor of the number of females that a particular geographic area can support, and McKinney et al. (2003) noted that the size and configuration of escape terrain is an important factor influencing sizes of bighorn sheep populations. Consequently, maintaining the integrity of historical lambing habitat is essential to the persistence of many populations of those specialized ungulates (Beecham et al. 2007).

Female bighorn sheep are unlikely to disperse from natal home ranges (Geist 1971*a*); therefore, disturbances near critically important areas are of particular concern (Papouchis et al. 2001). Disturbances near lambing areas can alter activity patterns (Leslie and Douglas 1980, Hamilton et al. 1982, Loehr et al. 2005) that may lead to abandonment of habitat (King 1985, Etchberger et al. 1989). Such reactions can have population-level consequences (Jorgenson 1988, Knight and Gutzwiller 1995) that often are not immediately discernible (Schoenecker and Krausman 2002, Oehler et al. 2005). Moreover, because most populations of bighorn sheep compose metapopulations, in which patches of habitat are important to long-term persistence at the level of the landscape (Bleich et al. 1996, Gross et al. 1997), abandonment of habitat is especially problematic if it causes individuals to leave preferred areas for an extended time (Bleich et al. 1994). Such responses would not only increase the probability of local extirpations (Gross et al. 1997), but would also diminish opportunities for connectivity and, thereby, jeopardize sustainability of the greater metapopulation (DeCesare and Pletscher 2006, Rubin et al. 2009).

The development of recreational trails in western North Dakota, USA, resulted in an unanticipated opportunity to examine questions related to the long-term effects of disturbance on wild sheep and the demographic consequences thereof. We evaluated public use near, or on, the Maah Daah Hey Trail (Trail) from 1995 to 2012, monitored distribution, abundance, and recruitment rates of female bighorn sheep for 12 years (2001–2012), and used retrospective analyses to determine whether the construction and subsequent use of that recreational trail adversely affected the distribution or demographics of bighorn sheep. We hypothesized that the sub-population of bighorn sheep at Sully Creek, where recreationists had unfettered access to lambing habitat and anthropogenic disturbances were commonplace, would exhibit differing dynamics when compared with 3 sub-populations not exposed to heavy recreational use, or that were spatially or visually separated from recreationists using the Trail. We therefore tested for differences in demographic parameters among those 4 sub-populations, one of which abandoned historical lambing habitat during our investigation (Sully Creek), and 3 others (Fantail Creek, Magpie Creek, and Summit Creek) that did not.

STUDY AREA

Our study area included portions of Billings and McKenzie counties in western North Dakota, where bighorn sheep had a discontinuous distribution near the Little Missouri River. Bighorn sheep occurred primarily on lands managed by the U.S. Forest Service (USFS) and on private or North Dakota state agency lands that were within the Little Missouri National Grassland (Grasslands).

Bighorn sheep exhibited a metapopulation structure, the result of the naturally fragmented distribution characteristic of those ungulates (Bleich et al. 1990); each sub-population occurred primarily in areas of steep, rugged terrain that were separated from similar areas by plains or rolling hills. The distribution of vegetation was consistent throughout the Grasslands and has been described previously in detail by Wali et al. (1980), Jensen (1988), Fox (1989), and Feist (1997). Elevations ranged from 637 m to 1,050 m, and substrates consisted of highly erosive silts and clays, sandstone, and scoria (Bluemle 1986). The climate was semi-arid, continental, and windy, with cold winters and warm summers; most precipitation occurred during April–September (Jensen 1974). Temperatures (which ranged from -36°C to 42°C during our investigation) and precipitation (which ranged from 15 cm to 50 cm) were essentially uniform throughout the study area (High Plains Regional Climate Center 2012; Table 1).

Primary land uses included livestock grazing, agriculture, and energy production. Recreational activities (hunting, biking, hiking, horseback riding, camping) also were common (Wiedmann and Hosek 2013). In addition to bighorn sheep, the study area was occupied by cattle and horses, mule deer, white-tailed deer (*O. virginianus*), pronghorn (*Antilocapra americana*), and elk. Potential

Table 1. Correlation matrix of mean monthly precipitation (above the diagonal) and mean monthly temperatures (below the diagonal) among 5 weather stations distributed throughout the study area in Billings and McKenzie counties, North Dakota, USA, 1948–2012.

	Precipitation correlations				
Station	**Medora**	**37 km NW Medora**	**2 km S Alpha**	**23 km S Watford**	**19 km E Watford**
Medora	—	0.981	0.999	0.990	0.938
37 km NW Medora	0.997	—	0.983	0.980	0.929
2 km S Alpha	No data	No data	—	0.964	0.899
23 km S Watford	0.999	0.998	No data	—	0.952
19 km E Watford	0.997	0.992	No data	0.997	—
			Temperature correlations		

predators of bighorn sheep included mountain lion (*Puma concolor*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), and golden eagle (*Aquila chrysaetos*).

The Trail, constructed in 1996, connected to 5 associated trails (Aspen and Ice Cave, Buffalo Gap, Cottonwood, Long X, and Summit) and to 7 developed campsites. The Trail and associated trails were 155 km and 73 km in length, respectively (Maah Daah Hey Trail Association 2012). Primary users of the Trail were hikers, equestrians, and mountain bikers (A. Warm, U.S. Forest Service, unpublished data). Segments of the Trail passed through, or were immediately adjacent to, lambing areas used by sub-populations of bighorn sheep at Fantail Creek, Magpie Creek, Sully Creek, and Summit Creek (Wiedmann and Hosek 2013; Fig. 1).

Strong correlations in precipitation and temperature throughout western North Dakota (Table 1), and similar fire histories (D. Svingen, U.S. Forest Service, personal communication), vegetation (Nelson 1961, Wali et al. 1980, Jensen 1988, Fox 1989, Feist 1997), distribution of avian (Tekiela 2003) and mammalian (Bailey 1926, Seabloom et al. 2011) predators capable of killing ungulates, and land uses (Wiedmann and Hosek 2013) across the Grasslands provided confidence that ecological conditions were similar among our study areas (Wiens and Parker 1995).

Historical Background

Bighorn sheep, a species native to western North Dakota, were successfully re-established in the state in 1956 and specifically to the Sully Creek area in 1962 (Knue 1991, McKenzie 1996). The sub-population at Sully Creek was stable and numbered between 20 and 30 individuals for nearly 3 decades (McKenzie and Jensen 1999), a period during which human activities were minimal and use of lambing areas by bighorn sheep was consistent from year to year (R. Johnson, North Dakota Game and Fish Department—retired, personal communication). Conditions changed in 1996 when the Trail was constructed and routed through a lambing area at Sully Creek.

During late spring each year from 2001 to 2005, we documented females and young moving southward 5 km from the Sully Creek lambing area nearest Medora to a more isolated site, where they remained for the duration of each of those lambing seasons. In 2006, no females used the lambing area nearest Medora, and only 2 of their 3 historical lambing areas were occupied that year. Because females could have abandoned the area because of intensive, off-trail recreational activities, the USFS rerouted that segment of the Trail, and then cut and burned stands of Rocky Mountain juniper (*Juniperus scopulorum*) in an effort to enhance habitat. We subsequently observed females with neonates return to that lambing area in spring 2007, but heavy off-trail use once again occurred, and the nursery band deserted that area shortly thereafter. Consequently, in 2008 the USFS blocked and refurbished much of the closed portion of trail to further dissuade recreational use. Females returned to this area in 2008, but off-trail recreational activity throughout the lambing area again resulted in displacement of bighorn sheep. During 2008–2012, females did not use the lambing area nearest Medora and appeared to have permanently abandoned that site; they had deserted it during 6, and abandoned it completely during 6, of the 12 years of our investigation.

The lambing area at Sully Creek was easily accessible and only 2 km south of the town of Medora and the South Unit of Theodore Roosevelt National Park (STRNP)—the most popular tourist destinations in North Dakota (Attractions of America 2014). Further, Sully Creek State Park was the southern terminus of the Trail and was adjacent to the lambing area at Sully Creek. Moreover, a substantial portion of that lambing area was transferred from private ownership to the USFS in 2000, 4 years after construction of the Trail. Prior to the transfer, off-trail use had been prohibited; after the transfer, however, opportunities for trail-users to roam unbounded throughout the entire lambing range were unconfined, because no regulation prohibiting such activity existed. Likely furthering the tendency for trail users to roam throughout the lambing area was the placement of a large sign at Sully Creek State Park that notified recreationists that the area was inhabited by bighorn sheep. Placement of that sign very probably increased use of, and forays from, the Trail as recreational users searched the area for bighorn sheep, activities that exacerbated harassment of females during late gestation or after parturition.

In contrast to the situation at Sully Creek, where the Trail was routed directly through a lambing area, trail segments through Fantail Creek, Magpie Creek, and Summit Creek were located >500 m from lambing habitat and substantial distances from either the north or south trailheads (Table 2). Moreover, the centroid of the lambing area at Sully Creek was <0.8 km from the Trail and only 1 km from the trailhead at Sully Creek State Park (Table 2). Recreationists were more apt to stay on the Trail at Fantail Creek, Magpie Creek, and Summit Creek, because they likely were unaware of bighorn

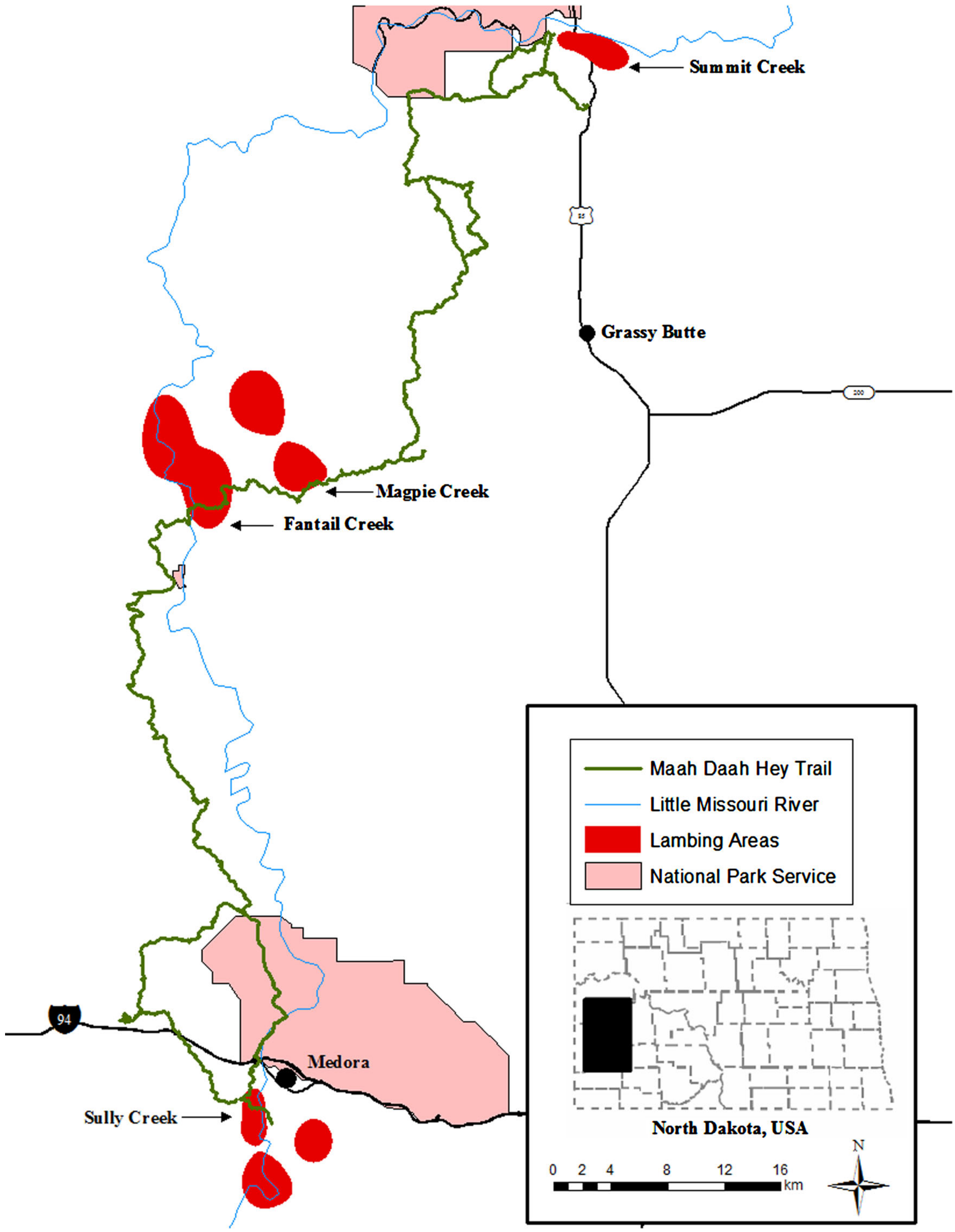

Figure 1. Distribution of 4 sub-populations in which female bighorn sheep were exposed to recreational activities associated with the Maah Daah Hey Trail, Billings and McKenzie counties, North Dakota, USA, 1996–2012.

sheep in those areas because the presence of those ungulates was not advertised. Spatial separation from the Trail (Table 2), combined with consistent and predictable behavior of recreationists, apparently was sufficient to preclude flight by bighorn sheep, thereby allowing females to acclimate to recreational activities and not abandon lambing habitat.

Our motivation for this research was to retrospectively examine the consequences of the increase in recreational use near Sully Creek relative to that experienced by the 3 other sub-populations during 1997–2012. For these reasons, we refer to the sub-population of bighorn sheep at Sully Creek as our treatment area (i.e., "highly disturbed"), and sub-populations at Fantail Creek, Magpie Creek, and Summit

Table 2. Distances (km) from the edges and centroids of 4 bighorn sheep lambing areas (LA) to trailheads, campgrounds, and the Maah Daah Hey Trail (Trail), Billings and McKenzie counties, North Dakota, USA, 1996–2012.

Sub-population	Distance from LA to south trailhead[a]	Distance from LA to north trailhead[a]	Distance from LA to campground[b]	Distance from centroid of LA to campground	Distance from LA to Trail[c]	Distance from centroid of LA to Trail
Summit Creek	155.0	0	0.55	3.14	0.60	3.10
Magpie Creek	74.8	80.2	0.92	3.25	0.52	1.54
Fantail Creek	60.5	94.5	8.62	10.18	0.65	2.65
Sully Creek	3.5	151.5	1.27	1.09	0	0.74

[a] Distance from edge of lambing habitat used by females to trailhead.
[b] Distance from edge of lambing habitat used by females to closest point of campground.
[c] Distance from edge of lambing habitat used by females to closest point of trail.

Creek as reference areas (i.e., "nominally disturbed"; Bowyer et al. 2003).

METHODS

During November 2000–February 2012, we used a hand-held net-gun fired from a helicopter (Krausman et al. 1985) to deploy very high frequency radiocollars (Advanced Telemetry Systems, Isanti, MN) on female bighorn sheep distributed among the 4 sub-populations. We examined each individual for clinical evidence of respiratory disease, and obtained tonsillar swabs opportunistically (Wiedmann and Hosek 2013). Although there were numerous sources of disturbance throughout the range of bighorn sheep in western North Dakota, we focused our efforts on the Trail, where recreational activity was most likely to occur (Fig. 1).

We maintained 2–3 females with radiocollars in each sub-population during 2001–2012 (Wiedmann 2011). We used a fixed-wing aircraft to locate marked females every 7–14 days from 2001 to 2012 using an Advanced Telemetry Systems R4000 receiver and 2-element antennae (RA-2AHS; Telonics, Inc., Mesa, AZ). We used telemetry locations and home range analyses to identify core-use areas, determine fidelity to lambing areas, and to obtain distributional information to facilitate population surveys.

We used a geographic information system (GIS) using a Fixed Kernel with a least-squares cross-validation bandwidth to determine the locations, number, and sizes of lambing areas for females in each sub-population (Rogers and Carr 1998). Lambing areas were defined as areas used by females from 1 April through July 31 annually. To control for the influence of non-maternal females, we used a 75% probability of locations obtained during April–July (2001–2012). Fidelity to lambing areas was determined by recording whether nursery bands used established lambing areas during April–July each year. Where females used multiple lambing areas, we measured distances between centroids of those patches as an index to movements by nursery bands during the lambing season.

We conducted a census of each sub-population twice annually (Wiedmann and Sargeant 2014) during late summer and the following March (2001–2012), and controlled for the few females translocated to or from 2 of the 4 reference sub-populations by reconstructing those sub-populations prior to analyses (Holl and Bleich 2009). We used a 60$\times$ power spotting scope to classify each individual as adult male ($\geq$2 yr old), yearling male, adult female ($\geq$2 yr old), yearling female, or young according to Geist (1968). We used data from the March census, as lambs approached 1 year-of-age, to estimate recruitment (Festa-Bianchet 1992, Holl et al. 2004, Wiedmann and Sargeant 2014).

We compared trends in public use in the vicinity of the Sully Creek lambing area (i.e., STRNP and Sully Creek State Park) and reference areas (i.e., North Unit of Theodore Roosevelt National Park [NTRNP]) by using Spearman's Rank Correlation (ρ) to compare visitor-days of use prior to and after the construction of the Trail. Further, we used the Kruskal–Wallis test, corrected for tied ranks (H_c), to determine whether an increase in mean annual use during spring occurred in the vicinity of the southern and northern termini of the Trail after its construction.

We adapted the "impact trend-by-time interaction" design described by Morrison et al. (2008:251) by using non-parametric techniques to make comparisons of demographic parameters between our treatment area and reference areas over the course of our investigation. We used the Freeman–Halton (F–H; 1951) Extension of Fisher's exact test (Zar 1984:393) to compare fidelity to lambing areas (i.e., use on an annual basis) and the number of years in which the finite rate of population growth (λ) was $\geq$1. We used the Kruskal–Wallis test corrected for tied ranks to compare recruitment rates among sub-populations (Zar 1984:176), and Spearman's Rank Correlation to test for trends in recruitment rates and in the number of female bighorn sheep within sub-populations (Zar 1984:318). We also calculated ρ to test for evidence of association between the number of females in each sub-population during summer (t) and recruitment rates the following March ($t+6$ months), and for a lagged relationship with recruitment rates 18 months later ($t+18$ months). Finally, we employed a one-tailed test for multiple proportions (Zar 1984:401) to compare the relative relationships of demographic parameters (% decline in population size, trend in recruitment rate, mean recruitment rate, and proportion of years $\lambda \geq 1$) among the 4 sub-populations. We acknowledge that these parameters were not completely independent, and we decreased alpha from 0.05 to 0.02 for this test (Bowyer et al. 2007).

We followed animal capture and handling guidelines of the North Dakota Game and Fish Department, as set forth by Foster (2005) and the Animal Behavior Society (2006). We dosed each captured bighorn sheep with 3 mL of ivermectin (Ivomec^{TM}; Merial Ltd., Duluth, GA) and 3 mL of Bo-Se^{TM} (Schering-Plough Health Corp., Union, NJ) and released them immediately.

RESULTS

After capture events during 2001–2012, we detected no clinical evidence of respiratory disease among the 44 females that we collared, and no virulent pathogens were detected among the individuals from which we obtained tonsillar swabs ($n = 18$; B. P. Wiedmann, unpublished data); 2 marked females from reference sub-populations were killed by mountain lions. There were no capture-related mortalities. We collected 1,893 locations from the radiomarked female bighorn sheep; sample size precluded a statistical comparison of the areas of lambing home ranges among sub-populations, but the mean size of lambing home ranges was 22.4 km^2 (SE = 5.2 km^2). Females typically arrived at lambing areas in early April, gave birth, and then formed nursery bands that moved cohesively among patches of lambing habitat during April–July. By late summer, loyalty to lambing habitat typically waned as females moved farther from the security of escape terrain and dispersed throughout their annual home ranges until the following spring.

After the opening of the Trail, there occurred a strong upward trend in public use (Spearman's Rho; $\rho_{14} = 0.832$, $P < 0.001$) in the vicinity of Sully Creek, the southern trailhead, as indexed by visitor-days recorded at the STRNP (National Park Service 2013). In contrast, there was no upward trend in use of the area in the vicinity of the northern terminus of the Trail ($\rho_{14} = 0.076$, $P_{1\text{-tailed}} = 0.389$), as indexed by visitor-days recorded at the NTRNP (National Park Service 2013).

No difference (Kruskal–Wallis test; $H_{1c} = 1.844$, $P = 0.175$) existed between mean use during spring each year prior to opening of the Trail in the NTRNP ($\bar{x} = 11{,}732$, SD = 8,680) when compared with mean use during spring prior to opening of the Trail in the STRNP ($\bar{x} = 14{,}562$, SD = 2,781). After opening of the Trail, however, there was a difference ($H_{1c} = 12.820$, $P < 0.001$) between mean annual use during spring as indexed by visitor days at the NTRNP ($\bar{x} = 7{,}443$, SD = 4,485) when compared with that metric for the STRNP ($\bar{x} = 15{,}925$, SD = 6,038).

Available data (National Park Service 2013) indicate that public use near Sully Creek State Park has experienced a constant increase since 2005, the earliest date at which use statistics were available on an annual basis ($\rho_6 = 1.00$, $P_{1\text{-tailed}} < 0.001$). Mean visitor use was far less prior to the opening of the Trail in 1996 ($\bar{x} = 19{,}400$ visitor-days/yr; $n = 2$) than after the opening ($\bar{x} = 30{,}163$ visitor-days/yr; $n = 7$).

Fidelity to lambing areas by females at Sully Creek (50.0%) was less (F–H Extension of Fisher's exact test; $P < 0.001$) than fidelity to lambing areas by females occupying the 3 reference areas, each of which was 100%. Overall recruitment in the Sully Creek sub-population ($\bar{x} = 0.15$ lambs/ad F, SE = 0.05) also was lower than the Fantail Creek ($\bar{x} = 0.38$ lambs/ad F, SE = 0.08), Magpie Creek ($\bar{x} = 0.34$ lambs/ad F, SE = 0.06), and Summit Creek ($\bar{x} = 0.39$ lambs/ad F, SE = 0.06) sub-populations (Kruskal–Wallis test; $H_{3c} = 8.082$, $P = 0.044$).

Females occurring at Sully Creek experienced a strong downward trend in recruitment rate during the study (Spearman Rank Correlation; $\rho = -0.705$, $P = 0.010$; Table 3); whereas, females from Magpie Creek ($\rho = 0.351$, $P = 0.263$; Table 3) and Summit Creek ($\rho = 0.347$, $P = 0.270$; Table 3), each exhibited a positive, albeit not significant, trend in recruitment rate. In contrast, data from females at Fantail Creek revealed a negative, albeit not significant, trend in recruitment rate ($\rho = -0.176$, $P = 0.584$; Table 3). No relationship existed between number of females during mid-summer and recruitment rate, either 6 or 18 months later, at Sully Creek or any of the reference sub-populations ($P > 0.250$ in all instances).

The number of females recorded during annual censuses at Sully Creek declined substantially during this investigation (−38%; $\rho = -0.210$, $P = 0.513$; Table 3); whereas, abundance of females at Fantail Creek (+50%; $\rho = 0.779$, $P = 0.005$; Table 3), Magpie Creek (+57%; $\rho = 0.528$, $P = 0.078$; Table 3), and Summit Creek (+60%; $\rho = 0.802$, $P = 0.003$; Table 3) exhibited strong upward trends. The proportion of years during which λ was ≥ 1 did not differ among Sully Creek and the reference sub-populations (F–H Extension of Fisher's exact test; $P = 0.286$). Nevertheless, a difference (one-tailed test for multiple proportions; $\chi^2_3 = 15.999$, $P = 0.001$) existed among the proportions of demographic values that were extreme for females at Sully Creek—which deserted or abandoned one lambing area during each of 12 consecutive years—compared to those values for the reference sub-populations, none of which abandoned lambing habitat (Table 3).

DISCUSSION

Only those females in the Sully Creek sub-population failed to use historical lambing areas throughout our investigation, likely the result of disturbance associated with the proximity

Table 3. Demographic characteristics of 4 sub-populations of bighorn sheep exposed to the Maah Daah Hey Trail (Trail), Billings and McKenzie counties, North Dakota, USA, 2001–2012. The Sully Creek sub-population deserted, and then abandoned, its traditional lambing area as a result of disturbance associated with unfettered recreational use of the Trail. Reference sub-populations (Fantail Creek, Magpie Creek, and Summit Creek) each demonstrated 100% fidelity to traditional lambing areas throughout the investigation.

	Demographic characteristics 2001-2012				
Sub-population	**Mean recruitment rate**	**SE**	**Percent population change**	**Years $\lambda \geq 1$**	**Trend in recruitment rate**
Fantail Creek	0.38	0.08	+50	8/10	−0.176
Magpie Creek	0.34	0.06	+57	8/11	+0.351
Sully Creek	0.15	0.05	−38	5/11	−0.705
Summit Creek	0.39	0.06	+60	8/10	+0.347

of intense human activity. The differences attributable to the Sully Creek sub-population when compared with similarities among the reference sub-populations, the environmental and ecological consistencies among the study areas, and our long-term data stream provide strong evidence that anthropogenic disturbance, particularly pedestrian traffic, altered demographic processes at Sully Creek. Indeed, no evidence of diseases that could have affected recruitment rates (Festa-Bianchet 1988, Foreyt 1990, Coggins and Matthews 1992, Ryder et al. 1992) was detected, and losses to predation were non-existent.

We did not detect a significant relationship between the number of females and recruitment rates in any of the sub-populations, indicating that density-dependent effects were not important in driving the observed dynamics. Moreover, similarities in climate, habitat, land uses, and fauna in areas occupied by the 4 sub-populations met assumptions described by Wiens and Parker (1995), and are inconsistent with the observed differences in demographic performance among the Sully Creek sub-population and the reference sub-populations. Movements by recreationists at Sully Creek were unfettered and occurred throughout the lambing area, and use in the vicinity of Sully Creek increased at a highly significant rate when compared with use near the reference sub-populations. Our indices to recreational use suggests that perturbations attributable to recreationists were less severe in the reference areas, especially during the lambing season, because those areas were substantially more isolated from concentrations of recreationists, the presence of bighorn sheep was not advertised, and trails were routed sufficient distances from lambing habitat, all of which discouraged recreationists from approaching bighorn sheep.

Recruitment rates differed significantly between females occurring at Sully Creek and those of the reference sub-populations. Additionally, a strongly negative trend in recruitment rate of the Sully Creek sub-population—which deserted or abandoned historical lambing habitat during each year of our investigation—was evident, and the number of females in that sub-population exhibited a strong downward trend. Moreover, rate of population decline, trend in recruitment rate, mean recruitment rate, and λ were all lowest at Sully Creek, whereas the percentage of population decline at Sully Creek was far greater than in the reference areas.

Despite the lack of significant differences among some demographic parameters, each of those from Sully Creek was the extreme value among the 4 sub-populations, yielding a highly significant result consistent with our contention that the Sully Creek sub-population performed far differently than the reference sub-populations. Further, upward trends in abundance in all but the Sully Creek sub-population indicated the absence of a density-dependent effect on population increases in the reference sub-populations.

Bighorn sheep did not habituate to anthropogenic disturbances at Sully Creek, where recreationists frequently strayed from the Trail, traversed lambing habitat in an erratic or unpredictable manner, and typically approached nursery bands closely and from above—an action that is especially threatening to bighorn sheep (MacArthur et al. 1982). Maternal females consequently were displaced from lambing habitat for 6 years, and abandoned it completely for 6 additional years. During that period, the Sully Creek sub-population clearly experienced demographic consequences in the form of declines in recruitment rate and population size while the reference sub-populations were characterized by high recruitment rates and increasing populations. The reference sub-populations apparently were not displaced from lambing habitat because spatial separation existed between bighorn sheep and recreationists, hikers did not stray from the Trail, and bighorn sheep were consequently not harassed.

Female bighorn sheep are especially alert when accompanied by neonates (Risenhoover and Bailey 1985) and may be particularly sensitive to disturbance during spring and summer—a period of intense recreational activity in western North Dakota—when young are at heel (Welles and Welles 1961, Horejsi 1976, Berger 1991, Bleich et al. 1994); moreover, they are especially sensitive to disturbances associated with cross-country travel by hikers (Papouchis et al. 2001). Females also are more likely to flee than males (Bleich 1999), and disturbances near habitat used by nursery bands may not only force females and young to move from preferred to more marginal areas (Feist 1997), but may also increase the likelihood of predation on lambs when away from rugged slopes (Berger 1991, Sayre et al. 2002). Such movements can also expose individuals to additional nutritional or energetic demands (MacArthur et al. 1979) as bighorn sheep feed farther from the safety of escape terrain (Risenhoover and Bailey 1985, Berger 1991, Schroeder et al. 2010). Consequent physiological, physical, or behavioral effects have population-level implications for abundance, survival, distribution, and habitat selection (Schwantje 1986, Belden et al. 1990, Bleich et al. 1994, Hayes et al. 1994). For example, young at heel, or even adults, can become vulnerable to predation as a result of decreased nursing or foraging efficiencies, further affecting survival rates (King and Workman 1986, Stockwell et al. 1991, Oehler et al. 2005).

Responses of bighorn sheep may not diminish after successive harassment events but, in those situations where sources of disturbance are non-threatening, consistent, and occur predictably, bighorn sheep have the capacity to acclimate (Geist 1971*b*; Hicks and Elder 1979; Jansen et al. 2007, 2009; Bleich et al. 2009). It should not be assumed, however, that bighorn sheep eventually will ignore perturbations where sufficient spatial separation does not exist, or where sources of disturbance are erratic or unpredictable (Papouchis et al. 2001). Fidelity to traditional lambing areas among our reference sub-populations indicates females either tolerated, or habituated to, recreational activities that were a sufficient distance from the security of escape terrain, and where hikers did not approach or harass bighorn sheep, especially during the lambing season.

Our results are consistent with those of Ciuti et al. (2008), who noted that the propensity of groups consisting of females and offspring to be sensitive to perturbations is widespread among ungulates. Indeed, Malo et al. (2011) reported that maternal groups (i.e., females with young) maintained a greater distance from pedestrians than did other social groups. Malo et al. (2011) further suggested the use of seasonal restrictions to minimize opportunities for pedestrians to approach maternal groups, and seasonal restriction of access to critically important areas at critically important times is an appropriate strategy to minimize detrimental effects to ungulates (Fairbanks and Tullous 2002).

Papouchis et al. (2001) reported that bighorn sheep responded most severely when hikers departed from established trails and traveled cross-country, or approached bighorn sheep directly; our results are consistent with reports of those investigators. Our data also agree with Holl (1982) and McKinney et al. (2003) that lambing areas are among the most important home-range attributes for bighorn sheep. Despite our inability to fully exclude other causative factors, our results are the first to provide insight into anthropogenic disturbance—particularly pedestrian traffic—affecting demographic processes among populations of bighorn sheep. Moreover, our results support the notion that the responses of bighorn sheep—and ungulates in general—are influenced greatly by the consistency, predictability, and level of threat associated with each source of disturbance (Graham 1980; Jansen et al. 2007, 2009; Bleich et al. 2009; Malo et al. 2011), rather than the mere presence of people (Ciuti et al. 2012) or other perturbations perceived as benign by those large mammals.

MANAGEMENT IMPLICATIONS

Determining the dynamics of a population decline can inform decisions about conservation priorities, and obtaining an understanding of the primary threat(s) causing a population decline are critically important to more effective conservation actions (Di Fonzo et al. 2013). Moreover, long-term and intense anthropogenic disturbance can cause shifts in habitat use that may not be detected until after habitat is abandoned (Longshore et al. 2013) and the demographic consequences become apparent. Wildlife advocates are challenged to develop strategies to conserve wildlife resources when decisions are made to provide recreational opportunities, as emphasized by Boyle and Samson (1985) and Fairbanks and Tullous (2002). To paraphrase Phillips and Alldredge (2000): To ensure a future for bighorn sheep, it is prudent to plan for recreational developments that minimally impact populations.

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