LONG-DISTANCE DISPERSAL AND POPULATION TRENDS OF MOOSE IN THE CENTRAL UNITED STATES

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ABSTRACT: Dispersal is a basic feature of the natural history of moose. Most information about moose dispersal pertains to short-distance movements because long-distance movements are uncommon and difficult to observe. Since the 1950s, moose populations have been increasing in Minnesota and North Dakota. This may have contributed to several long-distance dispersal events for moose that recently were reported in the central United States. These dispersal events provide an opportunity to investigate both the causes and the biological implications of this rare phenomenon. Herein, we review long-distance dispersal events based on information obtained from a variety of sources. Dispersal routes that could be measured included two with minimal distances of 1,511 and 367 km, plus several others that were shorter. These dispersal events and recent evidence of moose reproducing outside the current range of the species could be the result of increasing population trends of moose in the central United States. We suggest that the dispersing moose are founder individuals that are dispersing naturally from established populations in search of suitable habitats and mates in areas to the south. We hypothesize that this type of geographic range expansion is similar to that of moose when they dispersed across North America during the early Holocene. As moose continue to move south, wildlife managers should be aware of habitats within their respective states that might sustain populations of moose.

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Dispersal is a basic feature of the life history of most species. Local dispersal occurs within established populations of a species. It is important because it regulates population density, reduces intraspecific competition (Horn 1983), and minimizes inbreeding by promoting gene flow (Shields 1983). Short-distance, or diffusion (Pielou 1979) dispersal, is movement into suitable habitats adjacent to the currently occupied range of the species. This type of dispersal can lead to a gradual expansion of the range of a species. Long-distance dispersal differs from diffusion dispersal in that it may occur across large areas of unsuitable habitat. This type of dispersal can result in the discovery and colonization of isolated unoccupied habitats, and potentially the rapid expansion of a species' geographic range (Ricklefs and Miller 2000). Long-distance dispersal events are rare and thus difficult to observe in the field.

The moose (*Alces alces*) is the largest member of the family Cervidae and occurs primarily in the boreal forests of North America and Eurasia (Peterson 1955, Hall 1981). The overall geographic distribution of moose expanded in the late Pleistocene, with individuals dispersing from eastern Asia into North American via the Bering land bridge approximately 14,000-11,000 years ago (Hundertmark et al. 2002). At that time, glaciers in North America had begun to retreat, producing an abundance of the early successional habitats favored by moose and facilitating rapid expansion of the geographic range of the moose across North America (Reeves and McCabe 1998). Moose

are highly mobile with a strong propensity for dispersal (Geist 1971). Because of this mobility, they can disperse hundreds of kilometers in a short period of time. Dispersers are often, but not exclusively, young individuals (Hundertmark 1998). Young moose typically are abandoned by their dams after the first year, and juveniles tend to disperse only a short distance from their natal range (Gasaway et al. 1985) except in areas of high moose density (Ballard et al. 1991). Juvenile male moose tend to disperse farther from their natal range than juvenile females, and the percentage of overlap of home ranges between juvenile and dam is less for juvenile males than for juvenile females (Ballard et al. 1991, Cederlund and Sand 1992).

Although moose usually disperse short distances, long-distance dispersal events have been documented. For example, Mytton and Keith (1981) noted a 50-km dispersal distance for 4 young moose and a 250-km dispersal distance for a young bull moose in Alberta, Canada. Ballard et al. (1991) reported an adult cow that dispersed a distance of 177 km in southern Alaska. These accounts represent dispersal events within the geographic range of moose. To our knowledge, there have been few published accounts of long-distance dispersal of moose outside their geographic range. Miller et al. (1972) reported that a dead moose was found approximately 500 km north of traditional moose range in the Northwest Territories, Canada. In the central United States, Bowles and Gladfelter (1980) tracked the dispersal route of a bull moose from Minnesota through Iowa and into Missouri. They estimated that the total distance travelled was approximately 900 km. More recently, there have been several instances of moose dispersing outside their known range in the central United States. Peterson (1955) suggested that moose are still expanding their geographic range into areas that they have not occupied since the last glaciation. These long-distance dispersal records are important because they document a phenomenon that rarely is observed and potentially can provide insight into moose movements and biogeography.

As discussed above, technical reports on long-distance dispersal events by moose outside their normal geographic range are few. Most such information is found in popular media and newspaper articles, which, by themselves, provide little biological information. Herein, we present a summary of recent trends in moose populations in the central United States and of long-distance dispersal events by moose in this region. We discuss possible explanations for long distance dispersal by moose and potential biological implications of our findings.

METHODS

Information from primary literature, government documents, and Minnesota and North Dakota moose harvest reports were used to summarize recent population trends of moose in the central United States. To describe long-distance moose dispersal, we collected information regarding moose sightings and potential dispersal routes for North Dakota, South Dakota, Minnesota, Iowa, Nebraska, Missouri, Kansas, Oklahoma, and Texas. The sources consulted included newspapers, popular journals, books, primary literature, and communication with employees of the Kansas Department of Wildlife and Parks (KDWP), Nebraska Game and Parks Commission (NGPC), North Dakota Game and Fish Department (NDGFD), and South Dakota Game, Fish, and Parks (SDGFP). We feel confident in using non-biological sources, such as newspapers and popular journals, to document the movements of moose because moose are not likely to be confused with any other species.

In this paper, we consider the "historical" geographic range of moose in the central United States to be northeastern Minnesota (Peterson 1955). The "current" geographic

range consists of the "historical" range plus areas outside this region occupied in subsequent years as part of the recent expansion of moose in the central United States. We calculated dispersal distances from localities at the southern edge of the current geographic range of moose as mapped by Hall (1981) because it is likely that most long-distance dispersers came from populations in those regions. We obtained potential dispersal routes by connecting chronologically ordered localities and calculated dispersal distances using ArcGIS 9.0. Dispersal distances are considered to be minimal distances travelled because they were measured as straight lines between localities.

RESULTS

Population Status

When the north-central United States was settled by European immigrants and their descendents, moose occurred in northern Minnesota and northeastern North Dakota. However, by the early 1900s moose had been extirpated from North Dakota and northwestern Minnesota (Peterson 1955). Moose continued to inhabit the boreal forests of northeastern Minnesota although they undoubtedly were less abundant than they had been in pre-settlement periods. Because of this decline in moose numbers, Minnesota closed its moose hunting season after 1922 (Idstrom 1965). For the next 30 years, moose sightings were rare; however, in the early 1950s moose numbers began to rise and moose began to reclaim their former range in northwestern Minnesota (Karns 1998). Moose soon began moving back into North Dakota and, by the late 1960s, a small population inhabited the Pembina Hills in that state (Knue 1991). From there, they spread westward along the Canadian border to the Turtle Mountains and southward along the Red River Valley, where they inhabit the rugged lands of prehistoric Lake Agassiz (Karns 1998). By the 1980s, resident moose populations again occurred from northern and eastern North Dakota (Jones et al. 1983) across northern Minnesota (Jones and Birney 1988).

Because of the recent increase of moose, both North Dakota and Minnesota have established hunting seasons. Minnesota reopened its moose hunting season in 1971 (Karns 1998). Two units were available to hunters, in the Northwest and the Northeast, with hunting to be permitted in odd years only. Just 374 moose were harvested in 1971, but the number harvested in Minnesota continued to increase with considerably more moose being taken in the northwestern unit (Minnesota Department of Natural Resources 1990). For example, in 1983 a total of 780 permits were issued in the northwestern unit and 737 moose were harvested, as compared with 523 permits sold in the northeastern unit and 442 moose harvested (Minnesota Department of Natural Resources 1990). In 1985, a decrease in moose density was noticed in the northwestern unit. As a result, restrictions on moose hunting were implemented throughout the northwestern unit until 1997, when all moose hunting in the Northwest was closed. Since then, population numbers have remained low in the Northwest (Dickson 1998), and have remained essentially stable in the Northeast (Minnesota Department of Natural Resources 2005).

North Dakota implemented a moose hunting season in 1977, with a total of 9 moose being harvested (Knue 1991). Since then, harvest rates and hunting units have increased. In 1977, moose hunting was restricted to the two northeasternmost counties (Knue 1991). Today, hunting is permitted in the Pembina Hills, the Turtle Mountains, and the Red River Valley, which encompass the north-central, northeastern, and extreme eastern parts of the state extending as far south as the South Dakota state line (Knue 1991). Of the 3 main areas where moose occur in North Dakota, population estimates continue to be highest in the Pembina Hills area, followed by the Turtle Mountains, and then the Red River Valley

(Johnson 1990, Trego 1995). Harvest numbers of moose in North Dakota are more-or-less stable with 117, 129, and 116 moose harvested in 1989, 1994, and 2004, respectively (Knue 1991, Trego 1995, NDGFD 2005a).

Dispersal

Moose recently have been reported outside the current geographic range of the species in the central United States (Fig. 1). Some of those individuals dispersed over long distances. The most notable dispersal was undertaken by a young bull moose that was first reported in South Dakota and eventually dispersed as far south as Texas (Fig. 1). The first report was of 2 young bulls seen near Dell Rapids, South Dakota, in September 1987 (Wagner 1987). The two moose evidently became separated, because there were no reports of a second moose beyond Dell Rapids. In September 1987, one of the young bulls travelled across southeastern South Dakota, where it was reported near the towns of Alexandria, Dimock, and Parkston (for specific dates refer to Table 1, Dockendorf 1987). The moose crossed the Missouri River near Avon, South Dakota (Hornbeck 1987), and was reported a few days later in Page, Nebraska (Omaha World-Herald 1987). From there, it proceeded southward across Nebraska, passing near the towns of Elba, Palmer, and Chapman (Hornbeck 1988). The moose stayed in the vicinity of Grand Island and the Platte River for the remainder of the year and was spotted near Saronville, approximately 45 km southeast of Grand Island, on 8 January 1988 (Hornbeck 1988). The moose passed through Nelson and Guide Rock (Hornbeck 1988) before it was reported about 101 km to the southwest near Agra, Kansas, in late February (Kleinschmidt 1988). Laukaitis (1988) provided a detailed account of the moose's movement in Kansas. The moose remained in north-central Kansas, reportedly being seen near Kirwin Reservoir on the North Fork of the Solomon River (which is just south of Agra), for the remainder of the winter and into the spring. In June 1988, it was seen west of Stockton, approximately 45 km southwest of Agra. The moose remained in that area, possibly finding refuge from the summer heat at Webster Reservoir on the South Fork of the Solomon River (which is just west of Stockton), until September, when it was seen approximately 104 km farther south near Rush Center. From Rush Center, the moose quickly moved through south-central

Table 1. Time and locality information for the dispersal of a moose through South Dakota, Nebraska, Kansas, Oklahoma, and Texas. Numbers in paraenthesis correspond to those shown in Figure 1.

State	Reference Locality	Day	Month	Year
South Dakota	Dell Rapids (1)	15	Sept	1987
	Alexandria (2)	27	Sept	1987
	Dimock (3)	29	Sept	1987
	Parkston (4)	29	Sept	1987
	Avon (5)	1	Oct	1987
Nebraska	Page (6)	5	Oct	1987
	Elba (7)	13	Oct	1987
	Palmer (8)	16	Oct	1987
	Chapman (9)	18	Oct	1987
	Grand Island (10)	19	Oct	1987
	Phillips (11)	30	Oct	1987
	Trumball (12)	12	Nov	1987
	Harvard (13)	26	Dec	1987
	Saronville (14)	8	Jan	1988
	Nelson (15)	15	Jan	1988
	Guide Rock (16)	21	Jan	1988
Kansas	Agra (17)	22	Feb	1988
	Stockton (18)	18	Jun	1988
	Rush Center (19)	19	Sept	1988
	Kinsley (20)	20	Sept	1988
	Ashland (21)	22	Sept	1988
	Englewood (22)		Sept	1988
Texas	Perrytown (23)		Nov	1988
	Dalhart (24)		Nov	1988
Kansas	Ulysses (25)		Dec	1988
	Sublette (26)	5	Feb	1989

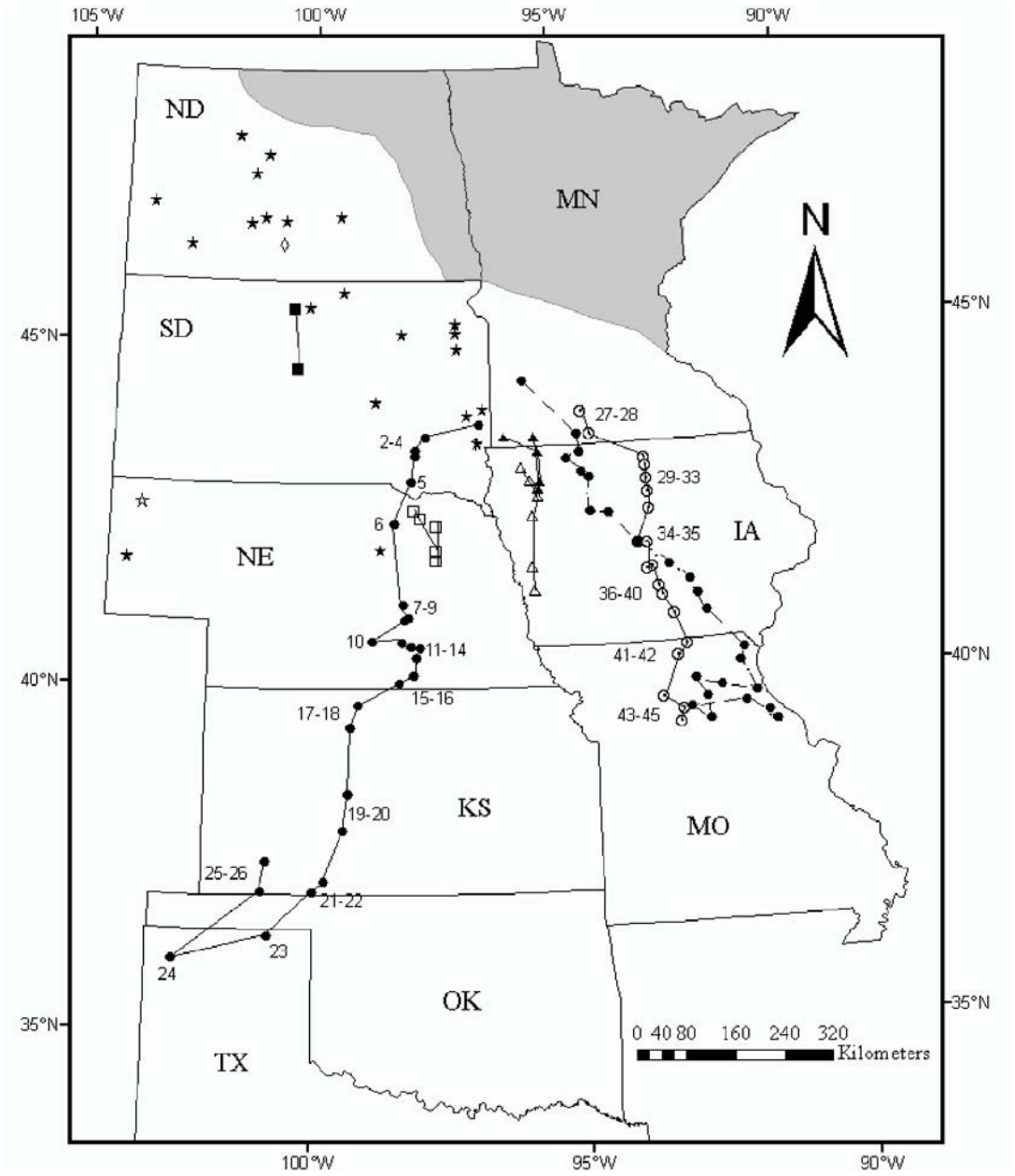

Fig. 1. Records of occurrences and potential dispersal routes of moose in the central United States. The gray area represents the current distribution of moose in this region as mapped by Hall (1981). Symbols connected by solid lines represent potential dispersal routes described in this study. The symbols connected by a dashed line represent a dispersal route described by Bowles and Gladfelter (1980). Solid stars depict individual records of moose in the central United States. The hollow star and diamond represent instances in which a moose remained in the area for an extended period of time. Numbers correspond to locality information listed in Tables 1 and 2.

Kansas, passing near Kinsley, Ashland, and Englewood. Although we were unable to find any reports of the moose having been seen in Oklahoma, it presumably passed through the Oklahoma Panhandle because it was next seen near Perrytown, Texas, in November and later near Dalhart, Texas (Unruh 1989). From this location, the moose reversed directions and returned to southwestern Kansas, where it was spotted near Ulysses in December 1988 (Associated Press 1989a). While it was in that area, a local veterinarian obtained permission from KDWP to tranquilize the moose. She claimed that the moose was in poor health and in need of medical attention. On 5 February 1989, the bull moose was tranquilized near Sublette, Kansas, and transported to the veterinarian's facility (Associated Press 1989b). No diagnosis was ever given as to whether or not the moose was, in fact, sick. After treating the animal, it apparently was released somewhere in Colorado (the exact location is not known). From first being observed near Dell Rapids, South Dakota, the moose travelled an estimated straight-line distance of 1,511 km. The time it took to travel this distance was 509 days, giving the moose an average speed of 2.9 km/day. The exact area from which this moose dispersed, and thus the total distance it moved, is impossible to know. However, the distance this moose travelled as measured from the southern edge of the current geographic range of the species was approximately 1,950 km.

In Iowa and Missouri, similar dispersal events by moose have been documented. Bowles and Gladfelter (1980) described a long-distance dispersal by a bull moose that began in southwestern Minnesota, continued through Iowa, and ended in the vicinity of Bowling Green, Missouri, near the Mississippi River (Fig. 1). A similar dispersal event took place in the same area a few years later (Fig. 1). In October 1986, a young bull moose was first observed in south-central Minnesota near St. James and, later in the month, near Fairmont, Minnesota (Alex 1987). The moose was first reported in Iowa near the town of Fertile in early November (Yost 1986) (for specific dates of sightings, refer to Table 2). From Fertile, the moose travelled directly south across Iowa, passing near Clear Lake, Thornton, Latimer, and Alden (Yost 1986). One week after being observed in Iowa, the moose was reported at Ames (Associated Press 1986a), where it passed near Nevada (Associated Press 1986b) and then down along Interstate 80 near Des Moines and over to Altoona (Alex 1986a). From there, the moose veered southeastward and passed near Pleasantville, northeast of the Melcher/Dallas area (Alex 1986b), and in early December was reported for the last time in Iowa in the vicinity of Georgetown and Melrose (Rins 1986). From first being seen

Table 2. Time and locality information for the dispersal of a moose through Minnesota, Iowa, and Missouri. Numbers in paraentheses correspond to those shown in Figure 1.

State	Reference Locality	Day	Month	Year
Minnesota	St James (27)		Oct	1986
	Fairmont (28)		Oct	1986
Iowa	Fertile (29)	2	Nov	1986
	Clear Lake (30)	2	Nov	1986
	Thornton (31)		Nov	1986
	Latimer (32)		Nov	1986
	Alden (33)	7	Nov	1986
	Ames (34)	9	Nov	1986
	Nevada (35)	11	Nov	1986
	NE of Des Moines (36)	18	Nov	1986
	Altoona (37)	18	Nov	1986
	Pleasantville (38)	30	Nov	1986
	NE of Melther/Dallas (39)	30	Nov	1986
	Georgetown/Melrose (40)	4	Dec	1986
Missouri	Omaha (41)	31	Dec	1986
	E of Pollock (42)	20	Jan	1987
	Hwy 139/Hwy 36 (43)	25	Jan	1987
	Chariton County/Chariton River (44)	4	Feb	1987
	Dalton (45)		Feb	1987

near Fertile, it took a little over a month for the bull moose to travel 335 km across Iowa. The moose then moved into Missouri, where it was spotted near Omaha in late December (Lamberto 1986). The moose was not reported again until approximately a month later, when it was seen east of Pollock, which is southwest of Omaha (Vance 1987). A few days later, the moose was observed near the junction of Highway 139 and Highway 36 (Alex 1987). From there, it moved southwestward into Chariton County, where it reportedly was seen near the Chariton River in early February (Alex 1987). The last report of this moose in Missouri was south of Dalton (UPI 1987). Since first being observed in south-central Minnesota, the moose travelled an approximate distance of 650 km. Because the exact dates when this moose was first and last seen are unknown, average dispersal speed for the entire trip was not calculated. However, we were able to calculate an average dispersal speed from where the moose was first reported in Fertile, Iowa, to where the moose was first reported in Missouri, near Omaha. The approximate distance travelled by the moose was 365 km in 60 days, giving it an average dispersing speed of 6.1 km/day. Again, the exact area from which this moose dispersed is unknown; however, the distance this moose travelled from the southern edge of the geographic range of the species was about 600 km.

Several other, shorter dispersal events were identified in southwestern North Dakota, South Dakota, Nebraska, Iowa, and Minnesota (Fig. 1). In South Dakota a young bull moose was reported near Mobridge (in the north-central part of the state), in November 1987. A few weeks later (in early December) it was seen north of Pierre (Woster 1987). In Nebraska, a bull moose was reported in the fall of 2000 near Verdigre (Tom Welstad, NGPC, personal communication). By December the moose had moved farther south to the vicinity of Creighton, and in January 2001 the moose had settled on the Elkhorn River near Battle Creek. For the next few months, the moose stayed south of Battle Creek in Madison County where it was observed feeding in a soybean field and on cattle feed (White 2001). However, in the fall of 2001, it appeared 40 km back to the north near Osmond. Reportedly, the moose was in poor condition and having trouble standing. Shortly after the moose died, the NGPC transported the carcass to the University of Nebraska-Lincoln Veterinary diagnostic lab for necropsy (Associated Press 2001a). The report concluded that cause of death was pneumonia and that, otherwise, the moose was in good physical condition (Dave Oates, NGPC, personal communication).

Several additional moose have been reported in Iowa in the past few decades, including 2 individuals that appeared in the northwestern part of the state and dispersed across western Iowa. The first was a bull moose seen in Sheldon, Iowa, on 23 September 1989 (Associated Press 1989c). The moose travelled southward near Paulina (Bullard 1989) and was seen on 25 September 1989 near Larrabee (World-Herald News Service 1989). A day later, the moose was reported northeast of Cherokee (Associated Press 1989d) and then, on 29 September 1989, it was seen near Cushing (World-Herald News Service 1989). On 8 October 1989, the moose was spotted near Woodbine (World-Herald News Service 1989). Finally, on 15 October 1989 it was reported near Underwood, where the moose was shot by a local resident (Alex 1989). Another moose was seen in Rock County, Minnesota, in October 1990 (Vosburgh and Peters 1991). The moose was reported near Ocheyedon, Iowa, on 23 October 1990 (Beach 1990). It then was observed farther south, near Sutherland, on 4 November 1990 (Associated Press 1990). The moose stayed in this area for about a month until it was reported again on 1 December 1990 near Larrabee (Stone 1990). The moose then headed back north, where it was hit by a car near Worthington, Minnesota, on 28 February 1991 (Vosburgh

and Peters 1991).

As moose increasingly occur in the central United States, it is of interest to ascertain if any individuals have found suitable habits in which to reside for extended periods of time. In this regard, a cow moose was seen near Crawford, Nebraska (indicated by the hollow star in Fig. 1), in the summer of 1974 (UPI 1974). The moose was seen again by hunters in the same area almost a year later in June 1975 (Nebraska Game and Parks Commission 1975). Finally, in August 1977 the same moose again was reported near Crawford (Lincoln Star 1977). Based on its last confirmed sighting in 1977, the moose had resided in this area for more than 4 years.

In another instance, a cow moose was reported inhabiting Oahe Wildlife Management Area (WMA), which is located along the Missouri River south of Bismark, North Dakota (indicated by the hollow diamond in Fig. 1; Bry 1981). In the summer of 1972, 2 cow moose were sighted wandering along the Missouri River just south of Bismark, North Dakota. Soon after, only 1 of the cows was seen at Oahe WMA. In November 1981, hunters found the moose lying down and unable to stand up, and a NDGFD biologist was called to Oahe WMA to euthanize the moose. From the first time the moose was reported at Oahe WMA until it died, the moose had lived in the area for 9 years.

As mapped by Hall (1981), the range of moose in North Dakota encompasses the entire extreme eastern part of the state. However, reproductive populations currently exist only as far south as Cass County, where, in 2001, a cow/calf pair was reported 25 miles west of Fargo (Bill Jensen, NDGFD, personal communication). Because no reproductive records have been reported south of this location, we conclude that populations located to the south of Fargo in Ransom, Richland, and Sargent counties consist only of vagrant individuals and no permanent populations. These vagrants appear to have spread into Roberts County in northeasternmost South Dakota. Reports of wandering moose in Roberts County have become common, with at least one moose being observed in that area each year (Higgins et al. 2000; Will Morlock, SDGFP, personal communication). Other reports indicate that moose are establishing reproductive pairs in central North Dakota. For example, in June 2005 a cow/calf pair was seen in Mercer County (Bill Jensen, NDGFD, personal communication). This report represents the westernmost reproductive record of moose in the central United States. Additional cow/calf pairs in North Dakota have been reported from Steele, Wells, and Sheridan counties (Bill Jensen, NDGFD, personal communication).

Since the early 1970s, several additional moose have been seen in the central United States (Fig. 1). We report noteworthy records in Nebraska, South Dakota, and North Dakota in Table 3. These accounts are not a comprehensive list of extralimital records of moose in the central United States. In fact, moose have become so common outside their current geographic range in North Dakota that biologists are only keeping reproductive records and have stopped tracking non-reproductive individuals (Bill Jensen, NDGFD, personal communication).

DISCUSSION

Dispersal Patterns

Our results suggest that certain dispersal patterns exist with regard to demographics and dispersal distance. For instance, the majority of long-distance dispersal events that occurred throughout the central United States appear to have been undertaken by young bulls in accordance with the process known as "jump dispersal". However, as proximity to regions inhabited by moose increases, the demographic composition of extralimital records changes. In areas of northeastern South Dakota, records of cow moose become more common and in western North Dakota several records of cows and cow/calf pairs

Table 3. Additional records of moose in North Dakota, South Dakota, and Nebraska. Dates with asterisks indicate a study that was conducted during the summers of 1976 and 1977, but no specific observation dates were given.

State	Reference Locality	Date seen	Citation
North Dakota	8 mi N, and 1 mi E of Ryder	6-Jul-71	Knue 1991
	E of Crystal Springs, on I-94	7-Oct-71	Knue 1991
	T134N, R95E, Sec. 5	26-Jul-72	Knue 1991
	7 mi E of Bismark	10-Aug-72	Knue 1991
	Crown Butte Dam	7-Nov-72	Knue 1991
	northern Billings County	1976/1977*	Seabloom et al. 1978
	notheastern McLean County	1976/1977*	Seabloom et al. 1978
	southern McLean County	1976/1977*	Seabloom et al. 1978
	southeastern Morton County	1976/1977*	Seabloom et al. 1978
South Dakota	near Flandreau	10-Oct-84	Sioux Falls Argus-Leader 1984
	Sioux Falls	15-Oct-89	Sioux Falls Argus-Leader 1989
	Mobridge	27-Sep-95	Svihovec 1995
	18 mi N of Watertown		Will Morlock, SDGFP, pers. comm.
	28 mi N of Watertown	Nov-95	Will Morlock, SDGFP, pers. comm.
	0.5 mi N, and 10.5 mi E of Eureka	18-Sep-95	Will Morlock, SDGFP, pers. comm.
	3 mi N of Watertown		Will Morlock, SDGFP, pers. comm.
	6 mi W of Conde		Will Morlock, SDGFP, pers. comm.
Nebraska	west of Scottsbluff	23-Aug-95	Lincoln Journal Star 1996
	3 mi NE of Rose	Apr-06	Aherns 2002

were reported. Female moose, especially cow/calf pairs, may be seen as undergoing diffusion dispersal in that they are dispersing relatively short distances from the established populations within the current geographic range of moose in North Dakota.

Causes of Dispersal

The increase in moose sightings outside their geographic range could be a direct or indirect consequence of an increase in population size. Peterson (1955) estimated that 341,700 moose inhabited North America, but the number of moose in North America had increased to 888,000 by 1987 (Kelsall 1987), and to 1,000,000 by 2000 (Timmermann 2003). Harvest population index records indicate that moose numbers in Minnesota and North Dakota have been at least sporadically increasing, and we suspect, based on published accounts of dispersal routes, that the populations in North Dakota and Minnesota are the source of most dispersing individuals in the central United States. However, it is possible that moose are dispersing into the central United States from other regions as well. The next closest populations of moose are those in the mountainous areas of Montana, Wyoming, and Colorado (Hall 1981). Individuals found in western Nebraska (Fig. 1) might have dispersed from those populations. For example, a yearling moose was sighted in Laramie, Wyoming, which is situated between the Laramie and Medicine Bow mountain ranges, in 2001 (Associated Press 2001b). The straight line distance from Laramie to Scottsbluff, Nebraska, where a bull moose had been seen in 1995, is approximately 160 km. Because moose are capable of travelling long distances (Hundertmark 1998; this study), it appears

possible that individuals can disperse from these areas into adjacent states.

When moose began appearing far to the south of their historical geographic range, several hypotheses were proposed by wildlife agencies and media to explain this phenomenon. The idea that a parasite, *Parelaphostrongylus tenuis*, causes long-distance dispersal in moose was suggested, primarily by the popular media, as the reason for this unusual behavior. *P. tenuis* is a nematode that causes a neurological disease known as "moose sickness" (Lankester and Samuel 1998). Moose become infected with *P. tenuis* by incidentally ingesting infected gastropods. In many accounts, witnesses claimed that dispersing moose appeared disoriented and lost, thus ultimately leading to the perception that the moose were sick. However, to our knowledge no study has confirmed moose sickness in any of the dispersing individuals. Anderson (1964) first described the effects on moose of the disease that *P. tenuis* causes. Symptoms included walking in circles, holding head and ears in abnormal positions, fearlessness, stumbling, deafness, blindness, paraplegia, and, in most cases, death. None of these symptoms suggest that long distance movements are a characteristic of this disease. Given the debilitating effects of this disease, especially on moose locomotory functions, it seems unlikely that infected moose would be physically able to disperse long distances.

Another possible explanation is that moose are leaving areas of high population density in search of other suitable habitat and mates. In presumed marginal habitats, such as along the periphery of their geographic range, densities of moose are lower than in areas located toward the center of their geographic range (Telfer 1984). This suggests that the surrounding areas in marginal habitat cannot support large populations of moose, and that it is necessary for moose to disperse to new habitats. Given their preference for early successional habitats, it seems plausible that moose would have evolved a dispersal behavior that would allow them to travel long distances in search of such habitats. Geist (1971) addressed this issue with his discussion of transient and permanent habitats. According to Geist (1971), transient habitats are those created by disturbance and are unstable and short-lived. Moose invade these areas shortly after disturbance and, as climax forest reestablishes itself, moose populations decline. Typically, disturbed habitats have a patchy distribution. Once an area is disturbed, species turnover rate is quite rapid and decreases as the community approaches climax (Shugart and Hett 1973). Thus, early successional habitats have relatively short life spans as compared with climax communities. In order to access these areas, moose would need to be very mobile.

Moose were probably one of the last species to immigrate to North America from Asia via the Bering land bridge (Reeves and McCabe 1998). From there, they spread rapidly across northern North America (Hundertmark et al. 2002). Different mechanisms by which species expand their range include jump dispersal, diffusion, and secular migration (Peilou 1979). Hundertmark et al. (2003) investigated the range expansion of moose by examining the genetic diversity of moose throughout their geographic range. They noted an overall lack of variation in mtDNA; however, haplotype composition was different between peripheral populations and populations inhabiting the central geographic range in North America. From this, they hypothesized that range expansion of moose occurred through a few founding individuals that dispersed from a pre-expansion population. Diffusion dispersal likely would not diminish genetic variation in this manner because of gene flow with populations in previously occupied areas. Rather, diminished genetic variation suggests that range expansion of the moose was the result of jump dispersal, or what Hewitt (1996) described as long-distance (i.e., leptokurtic) dispersal, where a few successful, long-dis-

tance dispersers founded new populations. Cronin (1992) supported this hypothesis as well, suggesting that founder effects were the cause of genetic homogeneity among the different subspecies of moose. Finally, this type of dispersal process agrees with Simpson's (1940) description of "sweepstakes dispersal", in which an individual disperses from an established population across a major barrier to another suitable habitat patch. Although, over time, numerous individuals attempt this sort of dispersal event, few are ever successful.

Our results favor the hypothesis that recent long-distance dispersal events by moose simply are the result of natural dispersal, rather than being induced by disease or other causes. If this is the case, the question then becomes what is the purpose for these dispersal events. We suggest that moose are dispersing from occupied habitats and searching for other suitable habitats. Consequently, we believe that moose are in the process of attempting to expand their geographic range southward and that this dynamic process is similar for most mammals. For example, Genoways et al. (2000) reported on extralimital records of the Mexican free-tailed bat (*Tadarida brasiliensis*) throughout the central United States. They concluded that pioneering individuals of *T. brasiliensis* occurring in areas outside their normal reproductive range are primarily foraging and exploring for new roost sites. They suggested that this is a natural process by which species may extend their geographic range. However, identification of active range expansion is difficult to discern and becomes apparent only in highly mobile and/or easily recognizable species. An example is the nine-banded armadillo (*Dasypus novemcinctus*), which recently has dispersed northward from Texas to the central Great Plains (Choate and Pinkham 1988, Taulman and Robbins 1996, Freeman and Genoways 1998).

The likelihood that long-distance dispersal will result in an expansion of range is small. Long-distance movements are rare and generally involve only one animal--often a male. The chance that both a bull and a cow (or a bull calf and heifer) will make a long move across unsuitable habitat to colonize the same new area is poor. The likelihood that diffusion dispersal will result in an expansion of range is much greater because of better reproductive opportunities. Nevertheless, it may be an evolutionary strategy of moose to send out expendable males to find new suitable habitats. Then, as the more reproductively valuable females disperse more gradually, they will find a bull already present in suitable habitat. This would prevent loss of reproductive potential by cows wandering around looking for a mate.

In conclusion, during the past 30 years there have been repeated records of moose occurring beyond their southern range boundary in the central United States. Most of these individuals consisted of solitary juveniles or young adults; however, there were some exceptions. We were able to track dispersal routes for some of the moose, whereas others were indicated by single locality records. This report documents the longest known distance a moose has dispersed from an established population. We conclude that these events were the result of natural dispersal that could lead to further expansion of their geographic range to the south. Further, we suggest that these dispersal events accurately represent the means by which moose expanded their range through North America during the early Holocene, as described by Hundertmark et al. (2003). Based on the assumption that most species share similar characteristics of range expansion, we believe that this phenomenon can serve as a model to illustrate how other species expand their geographic range.

Management Implications

The southward movement of moose in the central United States has management implications. Herein, we report two instances of moose inhabiting areas well outside the

current range of moose for an extended period of time—one in western Nebraska and one in southern North Dakota (Fig 1). These records are noteworthy because they indicate that there are areas to the south of the current geographic range that may sustain permanent moose populations. The primary limiting factor for moose in the southern parts of their geographic range reportedly is climate, particularly high temperatures (Kelsall and Telfer 1974, Renecker and Hudson 1986), in that moose experience heat stress at temperatures above 14-20° C. When heat-stressed, moose actively seek areas that provide them with shade and water for cooling (Schwab and Pitt 1991). Optimal forage is another important factor, although not as important as climate. Moose can adapt to a variety of forage, but in general they prefer shoots and other woody plants, such as willows (*Salix* spp.) and other early successional vegetation resulting from various kinds of disturbance, such as fire, logging, clearing, flooding, or glacial activity (Peterson 1955, Franzmann 1981). Other factors may include the density of deer in an area and human impacts, such as urbanization, extensive cultivation, and traffic. All these factors may work together to prevent dispersal events from resulting in an expansion of geographic distribution. Moreover, dispersal can cause expansion only if dispersers eventually find mates. Consequently, as noted above, the likelihood that a long-distance dispersal event will succeed is limited.

In central North Dakota, a cow moose inhabited Oahe WMA for at least 9 years. Oahe WMA consists of approximately 6,475 ha of Missouri River bottomland with good moose habitat that provides nearly continuous access to water and shade. Further, Oahe WMA is subject to frequent disturbances that enhance moose habitat. For example, in 1993, a 2,630 ha wildfire consumed parts of Oahe WMA (NDGFD 2005b). Because river bottomland usually has a large fuel load, it is susceptible to wildfires. Also, any subsequent flooding of the Missouri River would provide disturbed habitat for moose.

In northwestern Nebraska, a cow moose was reported living near Crawford for more than 4 years. Crawford is located within the Pine Ridge area where the habitat consists primarily of rolling prairies interspersed with pine forest. Several streams and ponds are located in the area, along with the White and Niobrara river valleys, which provide access to water for cooling (Telfer 1984). Little habitat in this area has been converted to agriculture because much of it belongs to the state and federal governments. Karns (1998) noted that moose do not fare well in areas where human intolerance for moose is high, thus moose tend to occur more often in areas that have not been highly developed. The Pine Ridge area is subject to frequent disturbances resulting from timber harvesting (Blyth et al. 1984, Alberts 2000) and, to a lesser extent, from prairie fires and occasional flooding along the White and Niobrara rivers. Because of the active suppression of wildfires, timber harvesting is currently the most important factor in that it stimulates production of early successional plant species (Krefting 1974), and increases the amount of edge next to these food sources. These areas, that combine edge and food, are favored by moose (Courtois and Beaumont 2002). Given that Pine Ridge is dominated by coniferous forest with a good supply of water and low human development, and given that a lone cow moose was able to survive in this area for more than 4 summers, it is possible that areas in the Pine Ridge area and the Niobrara River Valley may be capable of sustaining small populations of moose.

We thus suggest that areas with sufficient amounts of shade and access to water, supplemented by frequent disturbance that promotes new plant growth, potentially could serve as suitable habitats for moose populations south of their current geographic range. Areas similar to those described above that are located in adjacent states, such as the Black Hills of South

Dakota and areas located along the Missouri River and its tributaries in South Dakota, Iowa, Missouri, Nebraska, and Kansas, also might serve as suitable habitat for moose.

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