MOOSE POPULATION HISTORY ON THE NORTHERN YELLOWSTONE WINTER RANGE

Daniel B. Tyers

U.S. Forest Service, Gardiner Ranger District, P.O. Box 5, Gardiner, MT 59030, USA

ABSTRACT: Moose probably colonized the Northern Yellowstone Winter Range (NYWR) in the latter half of the 19th century. Euro-American settlement of the NYWR occurred at roughly the same time. Legislative protection of moose from hunting in the first half of the 20th century and suppression of wildfires facilitated moose population growth and range expansion. A hunting season in Montana along the northern boundary of Yellowstone National Park, authorized in 1945 in response to perceived damage by moose to willow stands, evidently reduced the moose population quickly and maintained it at moderate densities through 1988. In 1988, landscape-altering wildfires swept through the Yellowstone ecosystem and impacted old growth forest important for moose survival during winter. The moose population associated with the NYWR declined by 75% or more and has shown no sign of recovery by 2002. Several techniques for assessing population trend for moose on the NYWR were tested. Given the problems associated with monitoring a species at low densities with a dispersed social organization and occupying habitats where visibility is limited, aerial population censuses were not useful. A horseback trail survey, a road survey, and counts of moose in early winter or late spring in larger willow stands had greater potential as indices to moose population changes.

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The Northern Yellowstone Winter Range (NYWR) (Fig. 1) supports over half the wintering ungulates that utilize Yellowstone National Park (YNP) during summer (National Academy of Sciences 2002). While elk (*Cervus elaphus*) and bison (*Bison bison*) constitute more than 80% of the ungulate biomass on the NYWR during winter (National Academy of Sciences 2002), this winter range is essential to several less common ungulates, including moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), and pronghorn antelope (*Antilocapra americana*) (Yellowstone National Park 1997). In 1985, a study (Tyers 2003) was initiated to identify moose habitat needs and population status. This paper summarizes information collected on the history of moose on the NYWR and gives recommendations for monitoring the NYWR moose population.

Accurate assessment of ungulate population dynamics and factors that regulate populations is essential to sound population management (Gasaway et al. 1986, Van Ballenberghe and Ballard 1998). Obtaining reliable demographic information on any free-ranging ungulate population is difficult (McCullough 1984, Saether 1987), but moose are among the most difficult ungulates to monitor because they are the least social North American deer and frequently occupy habitats with poor observability (Schladweiler 1973, Houston 1974).

Moose population size is typically assessed in 3 ways- total area counts, sample estimates, and indices (Timmermann and Buss 1998). Timmermann and Buss (1998) advocated multiple information sources to assess population status. I used historic documents to trace the history of moose popula-

Fig. 1. Map of the Northern Yellowstone Winter Range study area showing prominent features and sampling areas. BCSU=Bear Creek Study Unit; YPSU=Yellowstone Park Study Unit; SCSU=Slough Creek Study Unit; SBSU=Soda Butte Study Unit.

tions on the NYWR and multiple population monitoring methods, including aerial surveys, horseback surveys, road surveys, and spatially restricted counts, to determine if vegetation changes associated with massive wildfires in the Yellowstone ecosystem in 1988 precipitated changes in moose population size. The results of my population monitoring efforts during 1985 – 2001 allowed me to evaluate the efficacy of several techniques for developing moose population indices and to identify reasonable techniques for monitoring future population trends.

STUDY AREA

The NYWR includes parts of YNP, the southern third of the Gardiner Ranger District, Gallatin National Forest, and mixed private and state lands (Fig. 1). The boundary of the NYWR is based on winter distribution of elk (Houston 1982). During this study, elk were the dominant ungulate species (10,000 – 25,000), but mule deer (2,000 – 3,000), bighorn sheep (100 – 200), bison (500 – 1,000), and pronghorn antelope (100 – 300) also occupied the NYWR. Moose numbers were unknown, but they wintered throughout the study area in scattered areas of suitable habitat, usually at higher elevations than elk.

Vegetation on the NYWR varies from low elevation (< 2,000 m) sage (*Artemisia* spp.) steppe to high elevation (3,000 m) coniferous forests. Willow (*Salix* spp.) stands occur along streams and in wet areas within forests.

Lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), Douglas fir (*Pseudostuga menzieisii*), and whitebark pine (*P. albicaulus*) are the most common coniferous species in the NYWR. The 1988 Yellowstone fires burned approximately 43,000 ha of the 143,900 ha of mature conifer forest present in the NYWR in 1988, thus converting about 30% of mature forest to early seral stages (Tyers 2003).

METHODS

Historical Documents

Agency files and archives were searched for statements on moose populations specific to the study area. Documents not considered by other authors that provided an historical context for population monitoring were of special interest.

Population Monitoring Techniques

Horseback transect index — In 1947, 1948, and 1949, Montana Fish and Game Biologist Joe Gaab looked for moose each September in the Absaroka Primitive Area (now the Absaroka Beartooth Wilderness) on about 177 km of trail. From 1985 to 2001, other observers repeated his route through the Hellroaring, Buffalo Fork, and Slough Creek drainages 34 times between July and late October to develop a moose population index.

Gaab rode primarily to look for moose. During 1985 through 2001, observers conducted other tasks along the routes (trail maintenance, hunter compliance checks, and outfitter camp inspections) but reported all moose observed. Gaab and more recent observers recorded age (calf or > 1 year of age) and gender (for moose > 1 year of age) of all moose sighted. From 1985 to 2001, the days spent covering the route ranged from 5 to 32, and trails were not traveled in any particular sequence. In both periods (1947-1949 and 1985-2001) observations were restricted to daylight hours and sightings were reported as number of moose seen per day per observer group. Observer group size varied from 1 to 6.

Road transect index — Moose sightings along the 89-km stretch of road from Gardiner to Cooke City, the only road in YNP maintained for wheeled vehicles year-round, were used as an index of moose distribution and abundance. Each trip was considered one sample regardless of the direction of travel. No attempt was made to standardize time of day, but at least 4 trips per month were completed in all months. Data collected between January 1987 – December 1992 and January 1995 – December 1997 were used to determine if there were differences in the number of moose seen seasonally and if moose numbers seen along the road differed before and after the 1988 fires.

To determine if changes between pre- and post-fire road counts were consistent across the NYWR, the road was divided into 5 sections. Each section consisted of a road segment that traversed similar vegetation and topography. The first section, Gardiner to Mammoth (8.0 km), included the Gardner River canyon. Topography was broken and the surrounding vegetation was arid grasslands and dry sagebrush unaffected by the 1988 fires. Gardiner was the lowest point along the road (1,585 m).

The second section was from Mammoth to Tower Junction (29.1 km). Topography and vegetation were diverse. Vegetation included open grasslands and Douglas fir, but there were also mature spruce-fir forests, isolated stretches of stunted willow and aspen, and 1 small area of insect-killed Douglas fir. Fires in 1988 raced across this area leaving a mosaic burn pattern in which many old tree stands were converted to young seral stages.

The third section extended from Tower Junction to Round Prairie (30.9 km). This stretch was mostly a broad open valley with expanses of grasslands and sagebrush along the Lamar River. Because most of this section was unforested, the 1988 fires did not cause much change in vegetative structure. The 1988 fires did not reach the fourth section, which extended from Round Prairie to Warm Creek (13.2 km) through mature lodgepole pine.

The fifth section, Warm Creek to Cooke City (8.0 km), followed Soda Butte Creek through the largest willow stands along the transect. The rest of the vegetation was mature lodgepole pine and spruce-fir. Only the area north of the road burned in 1988. Cooke City was the highest point along the road (2,134 m).

Willow stand overflight index — Barmore (1980) identified several willow stands where moose were frequently observed during aerial elk counts on the NYWR during 1968-1970. Two of the largest, Frenchy's Meadow in the Slough Creek drainage and the willow stands along Soda Butte Creek outside the eastern boundary of YNP west of Cooke City (Fig. 1), were selected for systematic sampling using fixed-wing aircraft. Each stand was flown between first light and 0900 twice a month year-round from 1987 through 1990. Three radio-collared moose in the Frenchy's Meadow area and 4 in the Cooke City area were available for use as a check on survey efficiency. All moose visible in and adjacent to the willow stands were counted on each flight. After counts were made, radio-collared animals were located to determine what proportion of radio-marked animals available in the drainage were in the willow stand.

Two indices of abundance were calculated for each flight: (1) number of moose observed (uncollared and radio-collared); and (2) the percent of available radio-collared moose seen. There were too few radio-collared animals to make valid estimates of total moose numbers in willow stands using mark-recapture methodology (Lancia et al. 1994), but the proportion of radio-collared animals seen did provide an estimate of the proportion of animals in the vicinity of the willow stands that were visible. Data from moose counts in willow stands were used to determine if moose numbers in favored willow stands varied among months or among years (including years before and after the 1988 fires).

Daily willow stand observations — Because over-flights of willow stands were limited in number and were restricted to morning hours, ground observations were used to better delineate the time of year and time of day that moose were most easily observed in willow stands. From April 1996 through June 1997, moose were counted and numbers recorded every half-hour daily, from first light until dark, in the willow stand between Silver Gate and Cooke City. Observations were limited to a standardized segment of the stand. These data allowed me to determine if counts from fixed wing aircraft were optimally timed (diurnally and seasonally) and provided another potential population index. To account for the changes in number of daylight hours through the year and occasional gaps in data collection, data were standardized as number of moose seen per number of observation attempts. Data were used to determine if moose were more likely to be sighted at specific times of day and/or in specific months.

Census flights — Data collected from road transects and willow stand flights suggested that moose were most observable around December 1 and May 1. Eight fixed-wing survey flights were scheduled in December and May 1988-1992. During the first 2 flights, pilots were told to follow transects (0.4-km parallel spacing on flat terrain and contour flying on slopes) as suggested by Gasaway et al. (1986). This approach was abandoned on subsequent flights because of difficulties following transects due to wind and topography, limited visibility due to dense forest canopy, and frustration by observers along unproductive sections. In the last 6 flights, searches were limited to areas where moose were most likely to be seen; the major willow stands along the northern boundary of YNP (inside and outside YNP). Stands were covered carefully on all 8 flights. Two fixed-wing aircraft were used for each flight with one covering the north half and one the south. Aircraft were flown about 97 – 113 kph at 61 – 152 m above the ground, depending on obstacles.

Statistical Tests

When assumptions on sample distribution were met (Zar 1999), the ANOVA module in the Statistica software package (StatSoft 1995) was used to test for temporal (hourly, monthly, seasonal, and/or annual) differences ($P < 0.05$) in willow over-flights and ground counts in willow stands. To test assumptions, data were first examined for outliers. Levene's test addressed homogeneity and Shapiro-Wilks' W test assessed normality. Questionable data were examined with histograms and scatterplots of means versus standard deviations. Data that did not meet the assumptions of ANOVA were tested using a Kruskal-Wallis test by ranks, for multiple treatments involving nonparametric data. Because the F-statistic is considered robust, the central limit theorem was invoked and ANOVA was used if data approximated a normal distribution and sample size was large ($n > 100$). A post hoc test, Student-Newman-Keuls, was used to look for differences among treatments when ANOVA demonstrated significance. P, F, Z, and H statistics are reported in this paper.

In analysis of road transect data, a 0/1 (present/absent) measurement scale was used to analyze the likelihood of observing ≥1 moose as an observer drove the road between Gardiner and Cooke City. Each trip (Gardiner – Cooke City or Cooke City – Gardiner) was considered an independent trial resulting in a set of 1,020 observations. Seasonal likelihoods were determined from analysis of 2-month periods (November/December, January/February, March/April, May/June, July/August, and September/October). An estimate of likelihood of sighting a moose each year during 1987 – 1992 and 1995 – 1997 was calculated by dividing trips with moose sightings by the total trips in a calendar year. To determine if differences between pre- and post-fire likelihoods of sighting moose were consistent over the entire transect route, individual road sections were compared over time using a Z-test ($P < 0.05$).

RESULTS

Historical Documents

The earliest reports on moose located in agency files did not include consistent assessments of population status in the northern areas adjacent to and within YNP during the early 1900s (Tyers 1981). McDowell and Moy (1942) reported that "old timers" regarded moose as a rarity in drainages along the north boundary of YNP between 1907 and 1915 while Rush (1942) reported that moose were considered "fairly common" by 1913 in the same area. In 1920, Stevenson (1920) noted that there were 13 moose wintering in 2 drainages currently designated as prime moose winter habitat in the NYWR (12 in Hellroaring and 1 in Buffalo Fork) and that the habitat would support more wintering moose than were present.

In 1921, the U.S. Forest Service began more extensive winter patrols (non-systematic snowshoe surveys conducted in December – April) to deter poaching and monitor wildlife near the northern boundary of YNP. Crane (1922) counted 16 moose during the winter of 1921 – 1922. Uhlhorn (1923) estimated 25 moose for the winter of 1922 – 1923. Johnson's (1925) report for 1924 – 1925 stated he could account for 65 moose. He noted that calf survival was high and believed the population was increasing.

By 1936, U.S. Forest Service reports (USDA 1936, McDowell and Moy 1942) expressed concern over the long-term status of willow stands associated with the NYWR and with the moose population that used them. These reports noted that willow condition was positively related to elevation and negatively related to access by elk and moose. The moose population wintering along the northern YNP boundary in 1935 – 1936 was estimated at 193 (54 in the Hellroaring, 80 in the Buffalo Fork, and 60 in the Slough Creek drainage). Over-winter utilization of willow in stands used by moose was estimated at 90%, and 75% of the willows in moose winter range were described as recently dead.

Montana Fish and Game Department personnel surveyed drainages north of YNP from summer through autumn 1942 (McDowell and Moy 1942). From June through October, they covered 341 miles (549 km) on foot and 1,341 miles (2,158 km) on horseback. They reported 194 unduplicated moose and suggested that moose had expanded their range into the area from YNP and that the population was increasing. They noted that >50% of willow plants were severely damaged in some areas where ungulates wintered while little or no degradation in willow stands was observed at elevations above ungulate winter range. They called for a controlled harvest of moose to prevent further damage to willow. Cooney et al. (1943) re-surveyed part of the area covered by McDowell and Moy (1942) in 1943 and reported an increase in moose numbers over that reported in the same area during the 1942 survey.

In 1942 and 1944, Montana Fish and Game Department employees conducted December or January moose surveys in the NYWR north of the YNP boundary (Parsell and McDowell 1942, McDowell and Page 1944). They found 10 – 15 moose utilizing major willow stands in and around Frenchy's meadow (Slough Creek drainage) but were surprised at the large numbers of moose occupying forested slopes adjacent to the willow stands. Parsell and McDowell (1942) estimated that elk and moose had utilized 90% of current willow growth by December 1942 and reported moose foraging on alder (*Alnus incana*), Engelmann spruce, lodgepole pine, and subalpine fir.

The 1945 Montana State Legislature passed Substitute Bill No. 41, which authorized the Montana Fish and Game Commission to "remove and dispose of moose increasing in numbers and damaging property by the limited license method" (Montana Fish and Game 1945). During the first hunting season, autumn 1945, McDowell (1946) reported that 40 permits were issued and hunters killed 35 moose across a hunting area that included most of the NYWR north of YNP (including the Hellroaring, Buffalo Fork, and Slough Creek drainages, and the Cooke City area). Reports of the impacts of hunting on moose varied. McDowell (1946) noted that a Forest Service employee reported 18 moose on a winter survey following the 1945 season, where Cooney et al. (1943) had counted 31 in winter 1943. McDowell (1946) believed this decreased count was most likely due to moose moving from one drainage (Hellroaring) to another (Slough Creek) due to declining willow production in Hellroaring. In a report submitted by McDowell and Smart (1945) describing a 1945 winter survey, the authors noted that 90% of the current year's willow production in some stands was utilized despite the harvest. In 1946, only 20 of 30 permits were filled and, at the request of local hunters and guides concerned about declining moose numbers, permit numbers were further reduced in 1947 (Couey 1947).

In 1947, 1948, and 1949 Montana Fish and Game biologist Joe Gaab conducted horseback surveys for moose and established an index of moose abundance (Gaab 1948, 1949, 1950). He traveled about 110 miles (177 km) of trail during September to count moose, using the same trails each year. He recorded 106, 71, and 30 independent moose sightings, respectively. In his opinion, the moose population was in a decline, which he attributed, in part, to a continued deterioration of willow stands (Gaab 1948, 1949, 1950). When interviewed in 2000, he stated that, during the first years of quota hunting, hunters shot "many more" moose than permits allowed, although 50 years later he could recall anecdotes but not actual numbers, nor could he find his field notes (J.

Gaab, Montana Fish and Game Department, personal communication).

Agency reports on moose population surveys and hunting seasons during most of the 1950s and 1960s were scarce. In 1963, Montana Fish and Game regulations listed a moose harvest quota in districts along the northern boundary of YNP of 45 with no restrictions on age or gender. A 1964 wildlife management plan for the Gardiner Ranger District, Gallatin National Forest (Kehrberg 1964), noted that addressing the "moose problem" (declining moose populations and deteriorating willow stands) in the Hellroaring-Slough Creek area was a management priority.

A different perspective on moose population/habitat trends from the 1920s to the 1960s was provided by Tony Bliss, co-owner of a small private parcel in Slough Creek near the large willow stand in Frenchy's Meadow. He summarized his observations of moose population trends (Kehrberg 1964: 9-10) as follows: "1926 to 1935 - lots of tall willow and few moose, elk and moose fed hay by Yellowstone Park in lower Slough Creek; 1935 to 1945 - more moose, still lots of willow, feeding ended about 1936; 1941 to 1945 - away at war; 1955 to 1962 - fewer and fewer moose and extensive loss of tall willow".

Stable values for indices of hunter effort (such as hunting days per moose harvested) suggested that the moose population remained relatively stable through the 1970s and early 1980s (T. Lemke, Montana Fish, Wildlife and Parks, personal communication). When this project began in 1985, the moose quota for hunting districts along the northern boundary of YNP was 55 with no restriction on age or gender. Quotas were reduced and restrictions implemented following extensive fires in the Yellowstone area in 1988. In 1990, the Montana Department of Fish, Wildlife and Parks issued 42 harvest permits (23 antlered and 19 antlerless) (T. Lemke, Montana Fish, Wildlife and Parks, personal communication). The quota was reduced to 21 (13 antlered, 8 antlerless) in 1991, in response to population declines observed during this study. Permits were reduced to 13 in 1996 (all antlered).

Population Indices

Horseback transect index — Gaab's (1948, 1949, 1950) 177 km transect in the Absaroka Beartooth Wilderness was re-run 34 times to develop an index of moose abundance during the years 1985 – 2001 (Fig. 2). The number of moose observed per day declined between 1947 and 2001. Only values in 1988 and 1989 approached sighting rates reported by Gaab. The total number of moose seen on surveys also declined. Gaab's counts averaged 69.0 (SD = 38.0, n = 3). Total counts in the

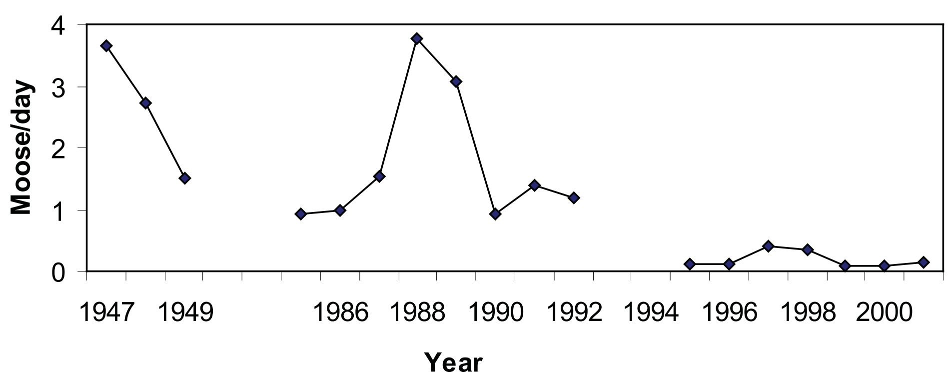

Fig. 2. Average number of moose seen per party per day during horseback surveys in the Yellowstone ecosystem 1947 – 1949, 1985 – 1992, and 1995 – 2001. In years with >1 survey (1992, 1995 – 2001), values are the mean of multiple surveys.

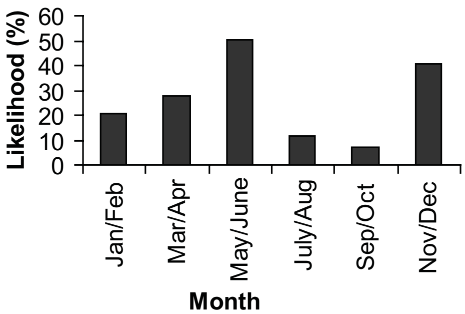

Fig. 3. Likelihood (%) of seeing at least 1 moose while traveling the road from Gardiner to Cooke City, Montana (89 km) by 2-month period for the years 1987 – 1992 and 1995 – 1997.

1980s prior to the extensive 1988 fires averaged 15.0 (SD = 4.4, $n = 3$). Post-fire counts in the late 1980s averaged 44.5 (SD = 6.4, $n = 2$). Counts in the 1990s averaged 6.0 (SD = 5.8, $n = 20$), and counts in 2000 – 2001 averaged 2.0 (SD = 2.8, $n = 9$).

Road transect index — The overall likelihood of seeing at least 1 moose while traveling the Gardiner to Cooke City road ($n = 1{,}020$) was 0.26 during the 9 years data were collected. The likelihood of seeing at least 1 moose per trip varied seasonally, with the maximum likelihood of sightings occurring during May/June when moose were observed on 50.4% of trips and lowest during September/October when moose were observed on only 7% of trips (Fig. 3). Because numbers of trips were relatively consistent across the six 2-month seasons and in individual years, analysis of pre- and post-fire effects and section effects were based on pooled data for individual years.

The likelihood of sighting a moose during a drive between Gardiner and Cooke City was highest in 1989 ($n = 84$ trips, likelihood = 0.49), the year immediately following the 1988 fires, and decreased in subsequent years (Fig. 4). The lowest likelihood of sighting a moose (0.02) occurred in 1995. There was a statistically significant decline in moose sightings (Z-test, $P < 0.05$) after the 1988 fires when a lag effect of a year was included in the test. Moose distribution along the road between Gardiner and Cooke City was not uniform before or after the 1988 fires (Fig. 5). No moose were seen in section 1 (Gardiner to Mammoth) before or after the 1988 fires. In section 2 (Mammoth to Roosevelt Junction), moose were observed on 15% of trips before the fires but only 4% after the fires, a significant decline (Z-test, $P = 0.04$). In section 3 (Roosevelt Junction to Round Prairie), the sighting incidence was 8% pre-fire compared to 1% post-fire, also a significant decline ($P < 0.01$). In section 4 (Round Prairie to Warm Creek), incidences of sighting were similar before and after the 1988 fires (5% and 6%, respectively; $P = 0.95$). The percentage of trips in which moose were observed in section 5 (Warm Creek – Cooke City) declined from 19% before the fires to 14% post-fire, but the difference was not significant ($P = 0.15$).

Willow stand over-flight index — Seventy-eight aerial searches of willow stands in Frenchy's Meadow and 73 in the Cooke City to Silvergate corridor were flown between June 1987 and December 1990. The average number of moose seen per flight did not vary significantly among the years 1987, 1988, 1989, and 1990 ($H = 1.95$, $P = 0.58$). The highest average number seen per flight was in 1988 (4.9), followed by 1989 (3.1). Results were the same for 1987 and 1990 (1.9 moose/flight). The difference in aver-

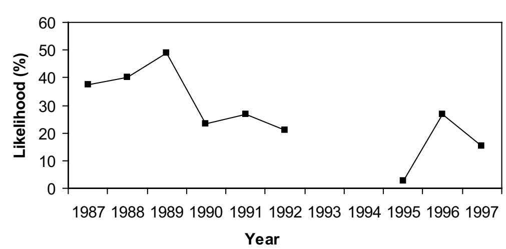

Fig. 4. Likelihood (%) of seeing at least 1 moose while traveling the road from Gardiner to Cooke City, Montana (89 km) for each of the years 1987 – 1992 and 1995 – 1997.

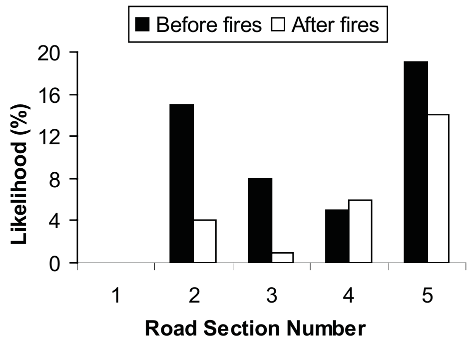

Fig. 5. Likelihood (%) of seeing at least 1 moose while traveling the 5 sections of road between Gardiner and Cooke City, Montana, prior to and after the 1988 Yellowstone fires. Section 1 = Gardiner – Mammoth (8.0 km); Section 2 = Mammoth – Tower Junction (29.1 km); Section 3 = Tower Junction – Round Prairie (30.9 km); Section 4 = Round Prairie – Warm Creek (13.2 km); Section 5 = Warm Creek – Cooke City (8.0 km).

age number of moose seen per month over 4 years was significant (H = 18.89, P = 0.026) (Fig. 6). The highest average number seen per flight was in November (9.3), followed by December (8.6), and May (7.6).

The percent of radio-collared moose available for observation (i.e., alive, in the drainage, and with operational radio-collars) seen per flight was not significantly different among years (H = 5.26, P = 0.15). Means for years varied from 0 (1987) to 12% (1988). Although no significant differences in the percent of collared moose observed by month were detected (H = 13.41, P = 0.15), the highest percent seen was in May (18.0%), followed by December (13.8%), and November (13.1%) (Fig. 6). This implies that in the late spring and early winter periods, when moose were most visible, < 20% of moose in a drainage were likely to be seen in fixed-wing surveys.

Daily willow stand observations — Daily counts of the number of moose in a willow stand near Cooke City were made at half-hour intervals for 15 months. The mean number of moose seen per half-hour of daylight varied significantly among months (F = 10.76, P < 0.001). The highest average number seen per half-hour was in June 1997 (0.9), followed by December 1996 (0.6), and May 1996 (0.6) (Fig. 7).

Counts of moose were highest on average at two times of day, between 0600 – 0930 hours and 2030 – 2130 hours (Fig. 8). When times were adjusted for seasonal changes in daylight, moose were most visible in the hours near sunrise and sunset. For months in late spring (May and June) and early winter (November and December) when highest numbers

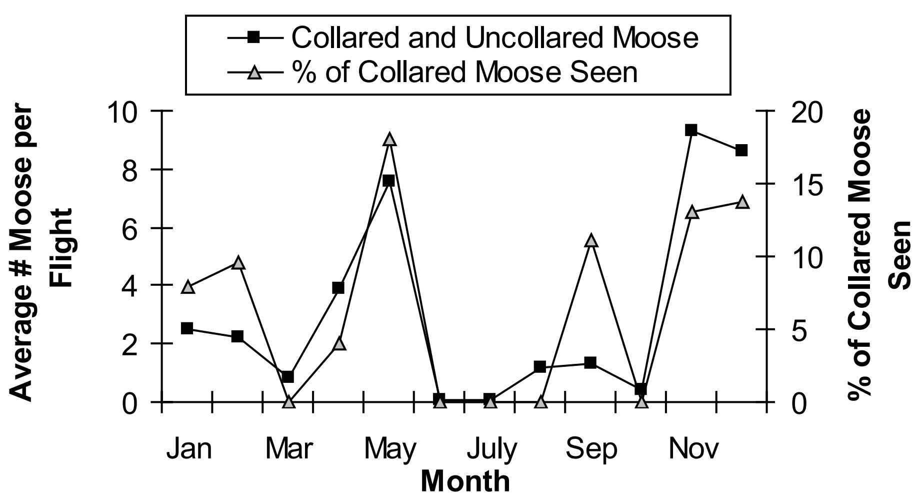

Fig. 6. Moose sighted during flights over willow stands along Slough Creek and near Cooke City, Montana, 1987 – 1990. Monthly averages for number of moose per flight and percent of collared moose seen are given in the figure.

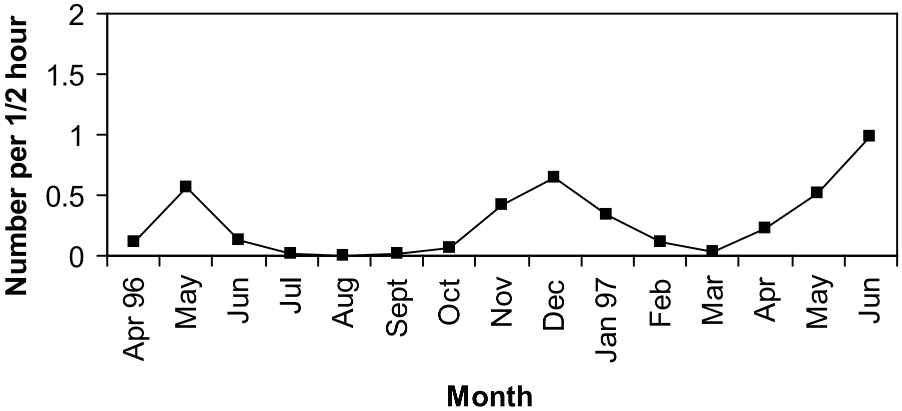

Fig. 7. Average number of moose seen per month (based on daily counts at half-hour intervals during daylight hours) in a willow stand near Cooke City, Montana, April 1996 – June 1997.

of moose per half-hour were recorded, the optimum times for moose observation were: May, 0600 – 0700; June, 0600 and 2130; November, 0730; and December, 0830.

Census flights – Even though the north and south halves of the study area could not be covered on all flights, the flights showed a sharp decrease in moose sightings between November 1989 and May 1990 (Fig. 9). The highest number seen on a single survey was 59 in November 1989. The lowest count (13) occurred in May 1992.

DISCUSSION

Population History

Long-term studies in North America support the idea that moose populations consistently erupt, crash, and then stabilize at various densities depending on prevailing ecological conditions (Mech 1966, Peek et al. 1976, Schwartz and Franzmann 1989, Loranger et al. 1991, Messier 1991, Van Ballenberghe and Ballard 1998). Geist (1974) attributed this pattern to a basic response by moose populations to changes in habitat quality. In his opinion, over the species' evolutionary history, moose have typically occupied limited areas of permanent habitat in low densities. When fire has created transient habitat, they have rapidly colonized these areas and reached comparatively high densities. Population eruptions can also be triggered by plant succession following logging and reduction of hunting or predation pressure, if a population is being held at low densities due to predation or hunting (Mech 1966, Peek et al. 1976, Messier 1991).

Moose evidently colonized the NYWR in the 1800s and initially increased in numbers in a manner similar to colonizing moose in other areas in North America, but the population did not respond positively to the massive

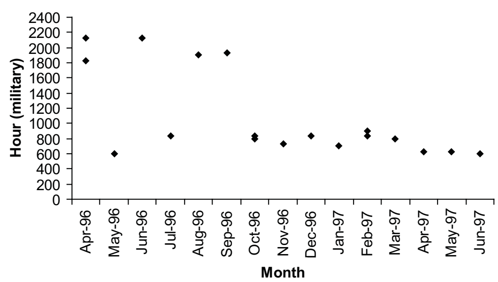

Fig. 8. Hours in which highest counts of moose in a willow stand near Cooke City, Montana were recorded by month, April 1996 – June 1997. Values are based on counts at half-hour intervals during all daylight hours. Months with 2 values indicate ties. Hour of the day follows standard conventions for mountain standard and daylight savings time.

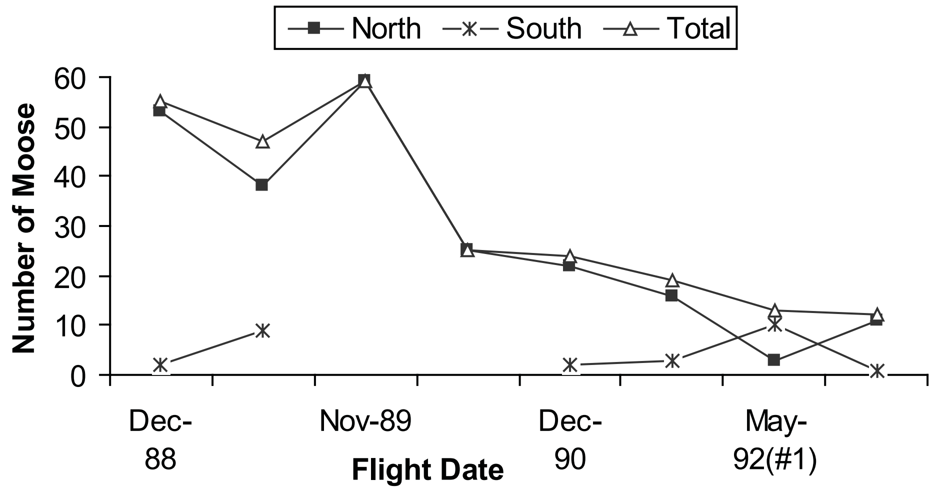

Fig. 9. Number of moose seen during aerial surveys of the complete Northern Yellowstone Winter Range (NYWR) and in 2 segments of the NYWR (north and south of the Yellowstone River) from December 1988 to May 1992.

forest fires that occurred in the Yellowstone ecosystem during 1988, as might have been expected based on Geist's (1974) theory and moose population responses to fire in Alaska (Schwartz and Franzmann 1989).

When moose invaded the NYWR, they encountered an environment in transition due to European settlement. Human predation was initially important and then curtailed. Forest succession was altered with attempts to suppress fires. Agency reports suggest that moose had expanded into all suitable habitats on the NYWR by the middle of the 20th century. Reports of negative impacts on willow stands (USDA 1936, McDowell and Moy 1942) indicate that, at least in some drainages, moose numbers may have stabilized or over-populated the area by the late 1930s. Regulated permit-based hunting, introduced in the 1940s to alleviate damage to willow stands on the NYWR, may have ended a population eruption triggered by a ban on hunting, dating from the early 1900s, and reduced predation resulting from concerted efforts to eliminate predators from the Yellowstone ecosystem during the 1910s – 1930s. Because no organized monitoring of moose populations was conducted by agencies from 1950 to 1985, the population trends during this 35-year period will never be known, but the horseback surveys conducted for this study from 1985 to 1987 produced similar moose sighting rates as Gaab's (1949) survey in 1949, perhaps indicating that the population remained relatively stable from 1949 to 1987.

The 1988 Yellowstone fires negatively affected moose habitat and population levels at a landscape scale. In the period immediately following the fires, winter 1988 – 1989 and summer 1990, some indices produced exceptionally high values for moose numbers. By winter 1990 – 1991, however, all indices indicated substantial declines in moose numbers. In areas where fire effects were severe, the reduction in numbers was greater than in areas where fire impacts were minimal. No sign of population recovery was evident through 2001; the last year data for 1 or more indices was collected.

Population Monitoring

The horseback surveys, road transects, and aerial surveys identified a decline in moose numbers following the 1988 fires. The willow over-flight index did not reveal any significant decline from 1987 to 1990, but revealed a similar pattern of change (relatively low in 1987, high in 1988 and 1989, low in 1990) to that provided by the horseback survey and the road transect.

The horseback transect index had high sighting numbers per day in 1988 and 1989 and consistent, very low sighting rates from 1995 to 2001. The high numbers of moose seen in 1988 and 1989 were probably due to increased sightability, when fires removed climax forests, and to movement of moose into unburned willow stands along the route. Data on moose movement and survival (Tyers 2003) indicate that data collected from 1996 to 2001 reflect a real decrease in moose numbers. The horseback transect index probably under-represented actual moose numbers before 1988.

The road-transect index generally mirrored results from the horseback survey; an increase in sighting likelihood in 1988 – 1989 and a decline thereafter. The decrease was most pronounced on the section where forests were most affected by fire (Mammoth to Round Prairie) and least pronounced where areas bisected by the road were not burned. No section had a significant increase over time. The post-fire decline on the road transect was apparent as early as 1990 while values from the horseback survey for 1990 – 1992 (post-fire) were similar to values for 1985 – 1987 (pre-fire). This may indicate that the road survey was more sensitive to population changes than the horseback survey or it may only be an artifact of sampling greater areas of burned terrain or more marginal habitat on the road transect than on the horseback survey.

Systematic aerial surveys were not initiated until the winter following the 1988 fires. Counts decreased substantially by 1990 and continued to decline until flights were discontinued in 1992. By 1992, numbers of moose sighted on aerial surveys were extremely low and limited to a few large willow stands, including those monitored in willow stand over-flights. Counts of moose obtained from willow over-flights indicated that variability on flights within the same stand, season, and year was so high that no significant decline was detected between 1987 and 1990.

The efficiency of indices employed in this study could potentially be improved by timing sampling to optimize moose sightability. Time of year can affect sightability of moose (Lynch 1975, Crête et al. 1986, Gasaway et al. 1986, Bisset and Rempel 1991). February and March are considered the most difficult months to find moose because they are more likely to be in dense cover (LeResche and Rausch 1974, Novak and Gardner 1975, Novak 1981). Sightability in November and December may be higher because moose form larger groups and have stronger preferences for vegetation with low, open canopies. This has been found in Alaska (Peek et al. 1974, Gasaway et al. 1986), Minnesota (Peek et al. 1974, Mytton and Keith 1981), Michigan (Peterson and Page 1993), Alberta (Lynch 1975), and Ontario (Bisset and Rempel 1991). However, 34 consecutive years of aerial surveys in Saskatchewan were successfully conducted in January and February (Stewart and Gauthier 1988).

In YNP, Barmore (1980) found seasonal variation in moose sightability during attempts to count moose incidental to elk distribution flights between 1968 and 1970. He concluded that moose were difficult to observe in this environment. Most moose Barmore (1980) saw were associated with willow, and he was most successful at finding them in these plant communities in May, early June, and December. In my study, radio-collared and uncollared moose were more likely to be observed from fixed-wing aircraft in early winter (November and December) and May than in other seasonal periods. A similar seasonal pattern was observed during intense ground sampling in willow stands near Cooke City.

Time of day also may influence visibility of moose (LeResche and Rausch 1974). Timmermann (1974) suggested from 1000 to 1400 hours as the optimal time for moose aerial surveys in Ontario. Peterson and Page (1993) preferred to survey moose in Minnesota just after sunrise. Data from half-hour counts in a willow stand near Cooke City for this study indicated that early morning (0600 – 0930 hours) and late evening (2030 – 2130 hours) were the best times of the day to see moose in the Yellowstone area.

Would aerial surveys in early winter or late spring, concentrated in early morning hours, provide an efficient means of monitoring moose associated with the NYWR at current population levels? Aerial surveys of moose have produced mixed results (LeResche and Rausch 1974, Stevens 1974, Novak 1981), but despite problems, counting moose on winter ranges from aircraft is still considered the most practical method for estimating moose numbers over large areas in North America (Mantle 1972, Gasaway et al. 1986, Gasaway and Dubois 1987, Timmermann and Buss 1998). In some areas, aerial surveys are very efficient. Edwards (1954) reported that 78% of moose located during intense ground surveys were seen from the air. Evans et al. (1966) reported that observers in fixed-wing aircraft saw 94% of moose observed by crews in helicopters. Gasaway et al. (1978) noted that 91% of radio-collared moose available to be seen were found during intensive searches from the air.

It is unlikely that fixed-wing aircraft used in a systematic survey of the NYWR would locate a high proportion of the moose population. Even in the months with highest sightability (November, December, and May), < 20% of radio-collared moose known to be in drainages containing preferred willow stands were observed from fixed-wing aircraft. High variability in both percent of radio-collared animals observed and in total animals observed indicate that using a large number of radio-collared moose to develop a sightability model, an expensive option that has had utility in estimating elk numbers (Samuel et al. 1987), is not likely to yield good results given the low density and low visibility of moose associated with the NYWR. Low density and low sightability would also limit the utility of helicopter surveys.

Developing an index of moose abundance using fixed-wing counts, or perhaps even ground counts, of moose in specific willow stands does have potential for tracking changes in the moose population associated with the NYWR, if counts are made in early winter or late spring and limited to early morning hours. Boundaries of key willow stands are easily identified (from the air or ground) and cover relatively small areas (most are < 40 ha). Counts of moose along the highway between Gardiner and Cooke City during early winter and late spring may also provide a relatively cheap means of monitoring population trends. Summer – autumn horseback surveys, especially when costs can be mitigated by combining counts with required tasks, such as trail maintenance and hunter management, may also be useful in tracking trends in moose populations. Although indices are less intellectually satisfying as a base for management of moose than statistically valid population estimates, indices may provide a reasonably reliable mechanism for determining population trends in situations where logistical constraints preclude accurate estimates of moose numbers.

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