Moose, *Alces alces,* Habitat Relative to Riparian Succession in the Boreal Forest, Susitna River, Alaska

William B. Collins[1], and D. J. Helm[2]

[1]Alaska Department of Fish and Game, 1800 Glenn Hwy., Palmer, Alaska 99645
[2]Agricultural and Forestry Experiment Station, University of Alaska Fairbanks, 533 E. Fireweed Avenue, Palmer, Alaska 99645

Collins, William B., and D. J. Helm. 1997. Moose, *Alces alces*, habitat relative to riparian succession in the boreal forest, Susitna River, Alaska. Canadian Field-Naturalist 111(4): 567–574.

We documented Moose, *Alces alces*, habitat characteristics relative to boreal forest succession in the Susitna River floodplain, Alaska. Early Shrub and Old Poplar (*Populus balsamifera*) Forest sites were most important to wintering Moose. Browse availability was the principal factor affecting winter habitat selection by Moose. Feltleaf Willow (*Salix alaxensis*) in Early Shrub was the principal browse species, producing approximately 101 kg/ha of browse. In a year of average snowfall, 76% of available Feltleaf Willow was utilized. Other important species, High Bushcranberry (*Viburnum edule*) and Rose (*Rosa acicularis*) were abundant in Old Poplar Forest and Birch-Spruce (*Betula papyrifera-Picea glauca*) Forest, but were unavailable when snow exceeded approximately 110 cm. Non-vegetated sites, dry sloughs and frozen river channels had significantly less ($p < 0.05$) snow accumulation than other sites, making them preferred paths of access during periods of deep snow. Wind speed did not vary significantly ($p < 0.05$) between successional stages older than Early Shrub, and wind did not appear to affect habitat use. Moose exhibited some preference for cover during periods of rest, especially during warm sunny days in late winter. While biologically feasible, enhancement of browse production in the Susitna River floodplain appears logistically impractical and of wrong priority. Habitat enhancement should be focused on upland sites where fire suppression has altered natural ecosystem functions, not in floodplain where the river continues to maintain a constant supply and diversity of successional conditions important to Moose and other wildlife.

Key Words: Moose, *Alces alces*, browse, cover, habitat, snow, vegetation succession, wind, boreal forest, Susitna River, Alaska.

Erosion and redeposition of land by glacial rivers are primary factors in maintaining the productivity and diversity of boreal forest and associated wildlife habitats (Larsen 1980). In regions where fire suppression is reducing the frequency and extent of forest rejuvenation and diversification, the perpetual influences of rivers and streams on forest vegetation and wildlife habitats are of increasing importance. Moose (*Alces alces*), Snowshoe Hares (*Lepus americanus*), Beaver (*Castor canadensis*) and other early successional wildlife are dependent on the availability of early growth hardwoods established following fire, fluvial events or other forest disturbances (Kelsal et al. 1977; Peek et al. 1976; Koehler and Brittell 1990). Not only do early successional wildlife depend on young hardwoods for food, but they can significantly affect successional development of boreal forest (Wolff and Zasada 1979; Bryant 1987; Pastor et al. 1988; Johnson and Naiman 1990; Helm and Collins 1997).

Glacial rivers flow through most major valleys in southcentral Alaska, occurring within important winter ranges of Moose. In the Susitna River valley, Moose prefer floodplain vegetation types in winter (Albert and Shea 1986). Wintering Moose are also attracted to low-lying uplands disturbed by recent fires, homestead or subdivision clearing, and right-of-way construction (Chatelain 1951; Albert and Shea 1986). Floodplains are mainstay habitat for Moose during severe winters, particularly in areas where lack of recent disturbance in upland forests has led to a decline in browse availability (Simkin 1975; Bishop and Rausch 1975).

Chatelain (1951) ranked the Susitna Valley as the most productive Moose habitat in Alaska. Chatelain observed that high Moose carrying capacity in floodplains of the Susitna River and its tributaries was further augmented by abundant upland browse resulting from wildfires and homestead clearing in the early and mid 1900s. By the early 1970s strict fire suppression and natural succession in old forest burns and homesteads had reduced browse availability causing Moose populations to decline (Bishop and Rausch 1974).

The objectives of this study were to document Moose habitat characteristics related to forest succession in the Susitna River floodplain and the boreal forest generally, and to identify how this riparian system may be best managed for Moose. We considered Moose to be a key indicator species (Hanley 1993), indicating availability of early successional habitat and welfare of associated wildlife.

Methods

We measured characteristics of Moose habitat for a range of successional conditions common to the lower Susitna River floodplain (62° N, 150° W). We made most measurements in a winter of average snow accumulation, 1992-1993, and in summer 1993. We noted general habitat conditions and differences in Moose distribution from 1981 to 1995.

Vegetation/habitat was represented by Early Shrub stages of early succession; Alder (*Alnus* spp.) and Young Poplar (*Populus balsamifera*) Forest stages of intermediate succession; and Old Poplar Forest and Birch (*Betula papyrifera*)-Spruce (*Picea glauca*) Forest stages of late succession. For more complete descriptions of these successional stages see Helm and Collins (1997).

We used a twig-count method (Shafer 1965) to estimate availability and utilization of browse. We identified browse as twigs occurring at least 0.5 m above the ground, on stems less than 4 cm dbh.

We point sampled horizontal cover in late winter and again in mid summer (Collins in press), by using an 8× monocular to sight the intersection of two lines on a target 1.5 m above the ground, 15 m from the observer. Overlap of the line intersection by vegetation indicated a point of cover. We also point sampled vertical cover in winter and summer, but by using an 8× rifle scope (mounted to a staff and viewed vertically through a 90° mirror reflection). Vegetation overlap of the cross-hair intersection indicated a point of cover.

Snow depth and hardness were measured with a Rammsonde penetrometer (Benson 1962; Coady 1974) at 24 - 30 locations within each vegetation stage, during winter 1992 - 1993 when snow depth fluctuated around the most recent 15-year average (Figure 1). We recorded wind speeds during a relatively strong wind. Successive measurements were made 1.5 m above the ground at 8 m intervals at 90 points arranged in a grid in each site. Each set of 90 recordings was completed simultaneously during a 15-minute period.

Using pellet-group counts (Neff 1968), we measured Moose use of different successional stages in spring, immediately following snow melt. We randomly located fifty belt transects (2 × 60 m) in three representative stands of each successional stage and searched for pellet groups deposited following leaf fall. When transect length exceeded the extent of a vegetation patch, we randomly relocated and completed the remaining portion elsewhere in the same vegetation patch.

Results

Early Shrub vegetation produced approximately 110 kg Moose browse per hectare, making it the most productive successional stage (Table 1). Feltleaf

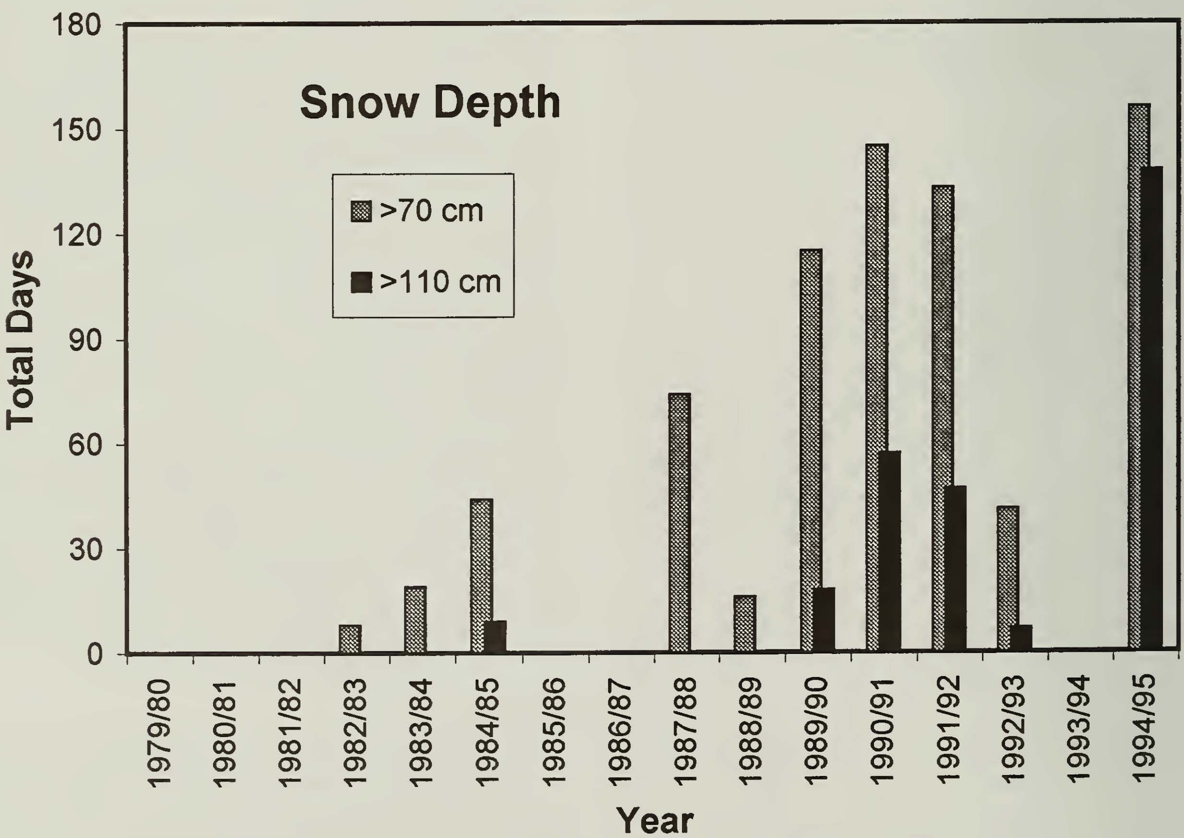

FIGURE 1. Snow depths at Willow, Alaska (White's Crossing), 1979-1995. Figure is based on data recorded by the National Oceanic and Atmospheric Administration. Deepest snow in vicinity of study area occurs at this location.

Table 1. Moose browse availability and utilization in different successional stages of the Susitna River floodplain. Means are followed by standard errors in parenthesis.

Stage Species Total	Diameter (mm) at point of browsing	Twig weight (g)	Twigs.stem^{-1}	Browsed twigs. stem^{-1}	Stems. hectare^{-1}	Available browse (kg.ha^{-1})	Browse consumed (kg.ha^{-1})	% browse utilized
Early shrub								
Populus balsamifera	4.7 (1.2)	1.53 (0.31)	3.80 (3.80)	0.49 (1.25)	1166 (680)	6.78	0.87	12.8
Salix alaxensis	5.4 (1.7)	1.90 (0.60)	6.15 (6.70)	4.61 (8.59)	8633 (2420)	100.88	75.62	75.0
Salix novae-angliae	3.1 (0.9)	0.52 (0.18)	2.85 (1.18)	2.69 (4.73)	1400 (937)	2.07	1.95	94.2
Total						109.73	78.44	71.5
Alder								
Rosa acicularis	3.9 (1.2)	0.64 (0.34)	2.06 (1.20)	0.29 (0.92)	117 (100)	0.15	0.02	13.3
Salix alaxensis	4.1 (0.2)	0.86 (0.37)	7.82 (8.12)	5.08 (3.94)	2684 (2700)	18.05	11.72	64.9
Salix novae-angliae	3.1 (0.9)	0.44 (0.18)	3.02 (2.41)	2.92 (1.59)	83 (66)	0.11	0.11	96.7
Viburnum edule	3.6 (0.8)	0.42 (0.29)	2.67 (1.95)	0.73 (1.40)	467 (247)	0.52	0.14	26.9
Total						18.83	11.99	63.7
Young poplar forest								
Rosa acicularis	3.9 (0.9)	0.92 (0.47)	2.35 (1.53)	1.44 (1.57)	1519 (957)	3.28	2.01	61.3
Salix alaxensis	4.9 (1.6)	1.63 (0.51)	6.27 (5.42)	5.02 (3.88)	352 (287)	3.60	2.88	80.0
Salix novae-angliae	3.1 (0.9)	0.47 (0.25)	3.26 (2.31)	3.15 (2.20)	37 (38)	0.05	0.05	96.6
Viburnum edule	4.1 (0.8)	0.72 (0.51)	2.80 (1.74)	2.36 (1.40)	463 (260)	0.93	0.77	82.8
Total						7.88	5.73	72.7
Old poplar forest								
Rosa acicularis	4.1 (0.9)	1.06 (0.49)	3.15 (2.44)	1.70 (2.25)	10750 (2197)	35.89	19.37	54.0
Viburnum edule	3.9 (0.9)	0.60 (0.43)	3.56 (2.65)	2.58 (2.39)	21833 (2897)	46.64	33.92	72.7
Total						82.53	53.29	64.6
Birch-spruce forest								
Betula papyrifera	3.3 (0.8)	0.44 (0.24)	9.90 (8.63)	2.52 (4.42)	750 (210)	3.27	0.83	25.4
Rosa acicularis	3.8 (0.9)	0.58 (0.31)	2.17 (1.15)	0.58 (1.03)	16933 (1863)	21.31	5.70	26.7
Viburnum edule	4.0 (1.2)	0.57 (0.45)	3.33 (2.52)	0.85 (1.76)	17066 (2610)	32.39	8.27	25.5
Total						56.97	14.80	26.0

TABLE 2. Horizontal[1] and vertical[2] cover (%) in different stages of riparian forest succession, Susitna River, Alaska. Measurements were made in March and July 1993. Means are followed by coefficients of variation in parentheses.

	Horizontal		Vertical	
Stage	Winter	Summer	Winter	Summer
Early Shrub				
8-yr-old	13.8 (37.7)	35.2 (27.3)	0.3 (10.8)	18.2 (49.2)
14-yr-old	28.2 (11.9)	62.0 (10.2)	8.6 (33.7)	68.0 (10.3)
Alder	24.9 (4.2)	55.5 (5.2)	11.2 (6.8)	65.0 (8.7)
Young Poplar Forest	26.0 (5.3)	46.9 (4.8)	14.8 (5.2)	62.4 (6.8)
Old Poplar Forest	23.0 (6.8)	51.2 (6.1)	23.4 (7.5)	52.1 (9.6)
Birch-Spruce Forest	25.1 (6.2)	48.7 (5.3)	22.2 (5.2)	61.3 (8.3)

[1]Horizontal cover = % visual obstruction within 15 m horizontal distance, 1.5 m above ground.
[2]Vertical cover = % visual obstruction of the sky as observed from 1.5 m above ground.

Willow (*Salix alaxensis*) represented 92% of available browse and 96% of browse consumed in Early Shrub. Our estimates of total browse and Feltleaf Willow availability for Early Shrub were almost identical to the most productive of similar sites measured in interior Alaska (Wolff and Cowling 1981).

Development of an Alder overstory was associated with reduced density and availability of Feltleaf Willow (Table 1). By this point in succession most Feltleaf Willow and Balsam Poplar surviving the combined effects of shading and browsing had grown beyond the reach of Moose, resulting in an 83% decrease in browse availability.

When sites were approximately 50 years age, Balsam Poplar dominated young forest overstories, and the density and availability of Alder and tall browse species had declined (Helm and Collins 1997). Although increases in Rose (*Rosa acicularis*) and High Bushcranberry (*Viburnum edule*) began to offset losses of tall browse species (Table 1), Young Poplar Forest was least productive of Moose browse.

Rose and High Bushcranberry increased when Balsam Poplar overstories opened as a result of tree mortality. This made Old Poplar Forests second only to Early Shrub in terms of browse production and consumption (Table 1).

By the time Birch-Spruce overstories had developed in late succession, density and availability of High Bushcranberry had declined by 78 and 70%, respectively. Rose increased in density by 58% but decreased in availability by 41% (Table 1). Shrub-sized Paper Birch produced limited browse in late succession.

Horizontal cover in winter, viewed 1.5 m above ground from a distance of 15 m, increased from 0 to 28% within the first 14 years of vegetation succession. It then remained relatively constant through all later successional stages (Table 2). Summer horizontal cover reached 62% in 14-year-old Early Shrub, but declined to approximately 50% in later succession.

Early Shrub provided little vertical cover in winter until approximately 14 years age, when canopies above 1.5 m height began to close (Table 2). Increase in size and density of White Spruce caused Old Poplar Forest and Birch-Spruce Forest to have the greatest winter vertical cover. Summer vertical cover was greatest in 14-year-old Early Shrub and Alder, declining slightly later in succession.

Mean wind speeds measured during winter 1.5 m above ground were greatest for river channels and gravel bars lacking above-snow vegetation (Table 3). Wind speed was significantly reduced in vegetated areas, with wind in Early Shrub being approximately 55% of that in barren areas. Wind speeds in Alder, Young Poplar Forest, Old Poplar Forests and Birch-Spruce Forest were approximately 22% of that in barren areas.

In late February 1993, snow depth in barren locations was significantly ($p < 0.05$) less than at all

TABLE 3. Mean wind speeds ($km \cdot h^{-1}$) during a relatively strong wind, 14 March 1993, within different stages of riparian forest succession, Susitna River, Alaska.

Stage	x	CV	minimum	maximum
Non-vegetated	8.8 a[1]	24.9	4	16
Early Shrub (8-yr-old)	4.8 b	57.4	1	10
Alder	1.9 c	47.3	0	4
Young Poplar Forest	1.9 c	48.0	0	4
Old Poplar Forest	2.0 c	44.2	0	4
Birch-Spruce forest	2.0 c	48.6	0	4

[1] Means followed by a common letter are not significantly different ($p < 0.05$).

TABLE 4. Mean depth (cm) and integrated hardness (kg-f cm) of snow within different stages of riparian forest succession, Susitna River, Alaska. Means are followed by coefficients of variation in parentheses. Measurements were made in late March 1993 following a winter of typical snow accumulation.

Stage	Hardness (kg-f cm)	Depth (cm)
Non-vegetated	4.76 (61.3)	48.1 a[1] (58.8)
Early Shrub (8-year-old)	1.96 (15.3)	83.0 b (4.5)
Alder	1.96 (14.3)	79.5 b (10.3)
Young Poplar Forest	1.95 (12.8)	77.9 b (8.5)
Old Poplar Forest	2.02 (13.4)	77.4 b (10.2)
Birch-Spruce Forest	2.12 (15.1)	75.7 b (11.8)

[1] Means followed by a common letter are not significantly different ($p < 0.05$).

other sites (Table 4). Snow depths in other successional stages did not vary significantly, although snow in Early Shrub tended to be deepest. We observed little variation in integrated snow hardness between vegetated stands, but barren sites were more than twice as hard.

Following winter 1992-1993, Early Shrub and Old Balsam Poplar Forest had the highest densities of pellet groups, 203 and 209 per hectare, respectively (Table 5). Alder had the lowest density of pellet groups, 108 per hectare. Assuming Moose consume an average of 5 kg dry weight per day during winter (Gasaway and Coady 1974) and that they use all areas for the same purposes, browse utilization indicated that Early Shrub was used 48% more than Old Poplar Forest. Pellet group densities were proportionately higher than percentages of browse utilization in Alder, Young Poplar Forest and Birch-Spruce Forest.

TABLE 5. Mean number of pellet groups per hectare (p.g. ha^{-1}) within different stages of riparian succession, Susitna River, Alaska. Pellets were counted in early May 1993. Estimates are based on 50 120 m^2 plots in each successional stage. Moose days per hectare (m-d·ha^{-1}) were estimated by: 1) dividing total p.g. by and assumed defecation rate of 20 p.g. $moose^{-1}$ day^{-1}, and 2) by dividing browse utilization (see Table 1) by an assumed forage intake of 5 kg $moose^{-1}$ day^{-1}.

Stage	p.g. ha^{-1}	m-d ha^{-1} (based on 20 p.g. $moose^{-1}$ day^{-1})	m-d ha^{-1} (based on 5 kg intake)
Non-vegetated	n.d.[1]	n.d.	n.d.
Early Shrub	203 (126)	10.2	15.7
Alder	108 (148)	5.4	2.4
Young poplar forest	161 (137)	8.1	1.1
Old poplar forest	209 (133)	10.5	10.7
Birch-spruce forest	160 (165)	8.0	3.0

[1]No data were obtained for non-vegetated sites because they included extensive snow and ice covered river channels and sloughs which were washed clean of pellet groups before snow had melted and pellet groups could be counted.

Discussion

Habitat

In all years, Feltleaf Willow was the principal browse resource for Moose wintering in the Susitna River floodplain. Not only was it highly preferred, as indicated by rates of utilization, but its availability was less limited by deep snow than were other species. Balsam Poplar saplings were available in all years, but were discriminated against by Moose except during periods of deep snow when other browse resources were less available.

Rose and High Bushcranberry were important browse species, but deep snow prevented their utilization in some winters. Moose utilized these species less in Birch-Spruce than in Old Poplar Forest, because those in the Birch-Spruce stands were shorter and smaller diameter and were bent over and covered by snow earlier than in Old Poplar Forest. Limited use of Rose and High Bushcranberry in Birch-Spruce Forest may also have resulted because those stands occurred primarily in the most stable portions of the floodplain, farthest from recently disturbed Early Shrub where Moose preferred to feed.

Highest percentages of browse utilization occurred in Young Poplar Forests, even though those stands were less productive of browse than any other successional stage. High pellet group density associated with numerous bed depressions indicated Moose preferred Young Poplar Forests and Alder stands for resting (Collins and Urness 1979 and 1981).

Alder and Young Poplar Forest may have been preferred resting sites for Moose because they provided better cover than many Early Shrub stands. Young Poplar Forest and Alder were successionally and spatially adjacent to Early Shrub where Moose preferentially browsed. However, requirement for cover did not keep Moose from utilizing preferred Willows within sparsely vegetated stands. Early Shrub isolated on small islands 100's of meters from other vegetation received utilization equivalent to

Early Shrub within a few meters of dense cover. The only other apparent preference of Moose for cover occurred in late winter on warm, sunny days.

In March and April, Moose frequently lay in the shade of mature White Spruce during sunny days, suggesting warmer temperatures and more direct sunlight caused them to seek shade to reduce heat stress (Schwab and Pitt 1991). Renecker and Hudson (1986) observed that Moose were more likely to show signs of heat stress than cold stress in winter. They observed increased metabolic rates of Moose when ambient temperatures exceeded -5.1°C, and observed Moose panting at 2.2°C. Demarchi and Bunnell (1995) similarly observed that cow Moose used denser forest during periods of heat stress in summer. Forage was not available beneath spruce and, therefore, we do not believe food attracted Moose to spruce as it sometimes does to upland spruce (LeResche and Davis 1973).

Moen (1973) concluded that reduction of wind velocity is one of the most significant benefits of cover to animals in winter, usually even more important than its effect on radiant energy flux. Nevertheless, we and Modafferi (personal communication) have not observed Moose increasing their use of denser cover in the Susitna floodplain during periods of wind. One-minute-wind speeds (National Oceanic and Atmospheric Administration, Climatological Data, Alaska, 1979-1995) exceeding 28.8 $km \cdot h^{-1}$, the limit to thermoneutrality for Moose calves at -20° C (Renecker et al. 1978), did not occur in March and April when Moose used Spruce cover.

Snow on barren gravel bars and ice-covered river channels was wind compacted and twice as hard as in vegetated sites, but did not support Moose. Except for winters 1989-1990, 1990-1991, 1991-1992 and 1994-1995 snow in these sites did not exceed the 70 cm depth Coady (1974) concluded represents a slight impediment to Moose. Consequently, braided river channels represented a network of corridors, providing Moose good access to all parts of the floodplain.

Besides elevating energetic costs to Moose, snow deeper than 70 cm (Figure 1) reduced browse availability. Rose and High Bushcranberry represented 22% and 29%, respectively, of all browse available in early winter, but they were buried when snow depth reached 70-110 cm. Snow greater than 110 cm caused Moose to stop browsing in forests by mid November in winter 1994-1995 and by late December in winters 1989-1990, 1990-1991, and 1991-1992 (NOAA).

Our estimates of Moose densities based on pellet group densities were subjective, since we did not determine defecation rates. We computed Moose densities, using a rate of 20 pellet groups per day (Andersen et al. 1992), because we assumed the quality and availability of forage in fall and early winter would have elevated food consumption and defecation rates above those determined in late winter by Franzmann and Arneson (1975), producing a season average closer to 20.

We became concerned about loss of pellet groups prior to counting, because Moose regularly used ice covered river channels and dry sloughs for access to feeding sites. We observed that spring flooding washed pellet groups away before snowmelt allowed pellet groups to be counted. Collins and Urness (1979) reported that Elk (*Cervus elaphus nelsoni*) defecated 11 to 18 times more frequently when traveling from one location to another, causing approximately 40% of all defecations to occur within 3.5 to 5.6% of the day as the animals were walking between feeding or resting sites. We concluded pellet groups could not be used to estimate overall Moose density in the floodplain but that they were useful in conjunction with other data for describing Moose distribution.

Browse utilization, tracks, beds and fecal deposition indicated only rare, localized summer use of the lower Susitna River floodplain by Moose. There were no indications of Moose in most areas in summer, an exception being use of several islands north of Talkeetna in late May and June. This agrees with Modafferi (1988) who observed a tendency for radio-collared cow Moose north of Talkeetna to leave the floodplain as snow receded but then to return for the period late May through June.

We believe that Moose are currently utilizing the lower Susitna River floodplain near winter capacity. During a year of average snowfall, Moose utilized preferred browse species at approximately 75%, a level Wolff and Zasada (1979) suggested represents carrying capacity for similar vegetation. Browse not utilized was apparently of poorer quality and/or less efficiently ingested. Although abundant reserves of less preferred browse species existed, snow depths exceeding 70-110 cm triggered several events that combined to decrease food availability and reduce Moose productivity and survival.

Deep snow eliminated availability of Rose, High Bushcranberry and short individuals of other browse species, confined Moose to the most accessible sites, and accentuated negative energy balance for Moose by causing them to expend greater energy for movement. Griese (*in press*) observed a 35% decline in the Susitna Valley Moose population following the deep-snow winter 1989-1990. Since that time, a continuing series of deep-snow winters has resulted in the population remaining at or below the 1990 level. Griese (*in press*) reported that Susitna Valley Moose have experienced significant winter die-off at least once each decade starting in the 1950s.

Management implications

Erosion and redeposition of substrates within a braided river system like the lower Susitna River is a dynamic process controlled almost entirely by discharge variations and sediment loads (Leopold 1964). Conditions necessary for vegetation succession to proceed are established as sedimentation elevates sites, reducing flooding frequency. Shifts of river channels quickly reverse succession, rejuvenating or eliminating browse stands (Helm and Collins 1997).

Unless flow of the Susitna River is interrupted by hydroelectric development, there is no need or reasonable opportunity to enhance browse productivity. While total area of floodplain covered by each successional stage may remain relatively constant over time, and while successional timeframes are generally predictable, life expectancies of specific sites are unpredictable. Eleven of 20 early successional sites we monitored were either temporarily denuded or completely eroded and redeposited down stream during the period 1981-1995, effectively rejuvenating them without human intervention. By contrast, browse production in upland sites can be efficiently and predictably enhanced by crushing, cutting, or prescribed burning (Oldemeyer and Regelin 1987; Collins 1996).

Browse production within Balsam Poplar Forest and Birch-Spruce Forest can be stimulated by a combination of overstory removal and scarification (Zasada et al. 1981; Collins 1996), costs being subsidized by timber sales. However, costs and accessibility make it difficult to justify overstory removal in floodplain solely to enhance browse production. Felling of Balsam Poplar and Birch must be followed by timely scarification to obtain hardwood density meeting minimal reforestation standards (Collins 1996). This requires use of heavy equipment during that time of year when it is not possible to construct winter roads or ice bridges to cleared sites. Browse regeneration failed in floodplain stands winter logged as much as 30 years ago, because the sites were not scarified, and preexistent Bluejoint Reedgrass (*Calamagrostis canadensis*) and Alder (*Alnus* spp.) increased to exclude other species (Mitchell and Evans 1966; Collins 1996). Tree harvest eliminated opportunity for natural scarification through uprooting by wind and gravity (Jonsson and Dynesius 1993; Helm and Collins 1997). Similarly, we observed regeneration failure in Young Poplar Forest where most Balsam Poplars were felled by Beavers.

The rapidity with which early seral vegetation in floodplains grows out of reach of Moose and/or the frequency with which it is rejuvenated by fluvial forces make it impractical to assess the welfare of Moose and their habitat by traditional methods of monitoring condition and trend (Stoddart et al. 1975). However, general assessment of browse within the floodplain indicates Moose are near ecological carrying capacity, being periodically limited by snow-induced shortages of food (Caughley and Sinclair 1994). Ecological carrying capacity of the Susitna Valley as a whole is primarily limited by fire suppression in lands adjacent to the floodplain.

Moose are limited by frequency of natural disturbances supporting establishment of early successional vegetation. Therefore, effective management must recognize the collective importance of all naturally occurring disturbances (erosion, forest diseases, windfall and fire) in maintenance of primary productivity within the boreal forest (Attiwill 1994). Managers should first attempt to enhance Moose habitat by eliminating or altering management practices which disrupt or prevent natural forces from maintaining diverse and productive habitat. Direct efforts to enhance habitat are not only more costly, but often, as on the Susitna River floodplain, misplaced.

Acknowledgments

This project is a contribution of Federal Aid Wildlife Restoration Projects W-24-3 and W-24-4.

Literature Cited

Albert, S. W., and **L. C. Shea.** 1986. Moose winter habitat in the lower Susitna Valley, Alaska: Pilot Project on Habitat Suitability Assessment. Alaska Deptartment of Fish and Game Technical Report, Number 86-6. 105 pages.

Andersen, R., O. Hjeljord, and **B. Saether.** 1992. Moose defecation rates in relation to habitat quality. Alces 28: 95–100.

Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63: 247–300.

Benson, C. A. 1962. Stratigraphic studies in the snow and firn of the Greenland ice sheet. U.S. Army Snow, Ice, and Permafrost Research Establishment/CRREL Report 70. 93 pages.

Bishop, R. H., and **R. A. Rausch.** 1974. Moose population fluctuations in Alaska, 1950-1952. Le Naturaliste canadien 101: 559–593.

Bryant, J. P. 1987. Feltleaf willow-snowshoe hare interactions: plant carbon/nutrient balance and floodplain succession. Ecology 68: 1319–1327.

Caughley, G., and **A. R. E. Sinclair.** 1994. Wildlife Ecology and Management. Blackwell Scientific Publications, Boston. 334 pages.

Chatelain, E. F. 1951. Winter range problems of moose in the Susitna Valley. Proceedings of Alaska Science Conference 2: 343–347.

Coady, J. W. 1974. Influence of snow on behaviour of moose. Le Naturaliste canadien 101: 417–436.

Collins, W. B. 1996. Wildlife habitat enhancement in the spruce-hardwood forest of the Matanuska and Susitna River Valleys. Alaska Department of Fish and Game Federal Aid in Wildlife Restoration Program Report, Project W-23-5, Study 1.44. 52 pages.

Collins, W. B. *in press*. Measurement of horizontal cover. Journal of Range Management.

Collins, W. B., and **P. J. Urness.** 1979. Elk pellet group distributions and rates of deposition in aspen and lodgepole pine habitats. Pages 140-144 *in*: Elk Ecology Symposium. *Edited by* M. S. Boyce and L. D. Hayden-Wing. University of Wyoming, Laramie.

Collins, W. B., and **P. J. Urness.** 1981. Habitat preferences of mule deer as rated by pellet-group distributions. Journal of Wildlife Management 45: 969–972.

Demarchi, M. W., and **F. L. Bunnell.** 1995. Forest cover selection and activity of cow moose in summer. Acta Theriologica 40: 23–36.

DesMueles, P. 1968. Determination of the number of pellet groups voided and the number of beds established by moose in winter. Le Nauraliste canadien 95: 1153–1157.

Gasaway, W. C., and **J. W. Coady.** 1974. Review of energy requirements and rumen fermentation in moose and other ruminants. Le Naturaliste canadien 101: 227–262.

Griese, H. J. *in press.* Survey-Inventory Management Report. Moose. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration, Project W-24-4, Study 1.0. Juneau, Alaska.

Hanley, T. A. 1993. Balancing economic development, biological conservation, and human culture: the Sitka black-tailed deer *Odocoileus hemionus sitkensis* as an ecological indicator. Biological Conservation 66: 61–67.

Helm, D. J., and **W. B. Collins.** 1997. Vegetation succession and disturbance on boreal forest floodplain, Susitna River, Alaska. Canadian Field-Naturalist 111: 553–566.

Johnson, C. A., and **R. J. Naiman.** 1990. Browse selection by beaver: effects on riparian forest composition. Journal of Forest Research 20: 1036–1043.

Jonsson, B. B., and **M. Dynesius.** 1993. Uprooting in boreal forests: long-term variation in disturbance rate. Canadian Journal of Forest Research 23: 2383–2388.

Kelsall, J. P., **E. S. Telfer**, and **T. D. Wright.** 1977. The effects of fire on the ecology of the boreal forest, with particular reference to the Canadian north: a review and selected bibliography. Canadian Wildlife Service Occasional Paper Number 32. Ottawa, Ontario. 58 pages.

Koehler, G. M., and **J. D. Brittell.** 1990. Managing spruce-fir habitat for lynx and snowshoe hares. Journal of Forestry 88: 10–14.

Larsen, J. A. 1980. The Boreal Ecosystem. Academic Press, New York. 439 pages.

Leopold, L. B., **M. G. Wolman**, and **J. P. Miller.** 1964. Fluvial processes in geomorphology. W. H. Freemen and Company, San Francisco. 522 pages.

LeResche, R. E., and **J. L. Davis.** 1973. Importance of nonbrowse foods to moose on the Kenai Peninsula, Alaska. Journal of Wildlife Management 37: 279–287.

Mitchell, W., and **J. Evans.** 1966. Composition of two disclimax bluejoint stands in southcentral Alaska. Journal of Range Management 44: 65–68.

Modaferri, R. D. 1988. Susitna Hydroelectric Project, Final Report Big Game Studies, Volume I - Moose - Downstream. Alaska Department of Fish and Game. 211 pages.

Moen, A. N. 1973. Wildlife Ecology. W. H. Freeman and Co. San Francisco. 458 pages.

Neff, D. J. 1968. The pellet-group count method for big game trend, census, and distribution: a review. Journal of Wildlife Management 32: 597–614.

Oldemeyer, J. L., and **W. L. Regelin.** 1987. Forest succession, habitat management, and moose on the Kenai National Wildlife Refuge. Swedish Wildlife Research Supplement 1: 163–179.

Pastor, J., **R. J. Naiman**, **B. Dewey**, and **P. McInnes.** 1988. Moose, microbes, and the boreal forest. BioScience 38: 770–777.

Peek, J. M., **K. L. Uruch**, and **R. J. Mackie.** 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildlife Monograph 48. 65 pages.

Renecker, L. A., and **R. J. Hudson.** 1986. Seasonal energy expenditures and thermoregulatory responses of moose. Canadian Journal of Zoology 64: 322–327.

Renecker, L. A., **R. J. Hudson**, **M. K. Christophersen**, and **C. Arelis.** 1978. Effect of posture, feeding, low temperature, and wind on energy expenditures of moose calves. Proceedings of the 14th North American Moose Conference and Workshop. Halifax, Nova Scotia.

Schwab, F. E., and **M. D. Pitt.** 1991. Moose selection of canopy cover types related to operative temperature, forage, and snow depth. Canadian Journal of Zoology 69: 3071–3077.

Shafer, E. L. 1965. The twig-count method for measuring hardwood deer browse. Journal of Wildlife Management 27: 428–437.

Simkin, D. W. 1975. Reproduction and productivity of moose. Le Naturaliste canadien 101: 517–526.

Stoddart, L. A., **A. D. Smith**, and **T. W. Box.** 1975. Range Management. McGraw-Hill, Inc. 532 pages.

Wolff, J. O., and **J. Cowling.** 1981. Moose browse utilization in Mount McKinley National Park, Alaska. Canadian Field-Naturalist 95: 85–88.

Wolff, J. O., and **J. C. Zasada.** 1979. Moose habitat and forest succession on the Tanana River flood plain and Yukon-Tanana upland. *In* Proceedings of the North American Moose Conference and Workshop. *Edited by* H. G. Cumming. School of Forestry, Lakehead University, Thunder Bay, Ontario 15: 213–245.

Zasada, J. C., **L. A. Viereck**, **M. J. Foote**, **R. H. Parkenson**, **J. O. Wolff**, and **L. A. Lankford Jr.** 1981. Natural regeneration of balsam poplar in the Susitna Valley, Alaska. Forestry Chronicle 57: 57–65.

Received 2 November 1995
Accepted 3 March 1997