EFFECTS OF VARIABLE FIRE SEVERITY ON FORAGE PRODUCTION AND FORAGING BEHAVIOR OF MOOSE IN WINTER

Rachel Lord[1] and Knut Kielland[1,2]

[1]Department of Biology and Wildlife, University of Alaska, Fairbanks, Alaska 99775-7000, USA; [2]Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775, USA

ABSTRACT: The increasing frequency and extent of wildfires in Alaska over the last half century has spurred increased interest in understanding the role of post-fire succession on vegetation establishment. Our primary goal was to examine how wildfire affects production and distribution of winter forage for moose (*Alces alces*) in interior Alaska, and how these changes in forage availability control forage offtake. Fire severity classification was based on post-fire depth of residual soil organic matter. We used a browse survey protocol to estimate the biomass of current year production (kg/ha) and over-winter offtake (kg/ha) by moose. Under the assumption of homogenous effects of fire severity on regeneration, we estimated that moose consumed 36% of all forage (current annual growth) across the study area. However, we found that moose exhibited significantly higher browse consumption relative to browse production in high fire severity sites than in low severity sites ($P < 0.05$). When we adjusted our estimates of forage production and consumption by accounting for the significant differences in browse consumption between severity classes and their distribution across the burn, moose consumed approximately 49% of available forage. Assessments of fire severity and its spatial distribution through remote sensing techniques and on-the-ground sampling provides improved projections of vegetation regeneration pathways following wildfires, and thus refined estimates of future browse production and habitat quality for moose.

Fire is the primary disturbance in Alaska's boreal forest, burning on average more than one million hectares annually (Dyrness et al. 1986). The post-fire landscape may be composed of a higher proportion of early successional stands, where successional pathways have led to deciduous species colonizing areas that were previously dominated by black (*Picea mariana*) or white spruce (*P. glauca*). This mosaic of vegetation directly affects winter foraging and habitat use patterns of moose (*Alces alces*). Numerous studies have investigated the effects of fire on population dynamics, habitat, and foraging of herbivores (Riggs and Peek 1980, Canon et al. 1987, Kilpatrick and Abendroth 2000) including moose (Peek 1974, MacCracken and Viereck 1990,

Weixelman et al. 1998, Maier et al. 2005). The purpose of this study was to assess the influence of fire severity, defined here as the amount of soil organic matter (SOM) remaining after the fire event, on the differential regeneration of plant species post-fire within the context of moose habitat. Secondly, we examined these effects on moose forage consumption in winter within a burn.

Biotic and abiotic factors influence the spatial distribution of forest regeneration following wildfires (Pastor et al. 1999, de Groot et al. 2003, Hellberg et al. 2003, Wisdom et al. 2006), with fire severity playing an important role in post-fire secondary succession. Fire events can increase diversity and density of plant species within the first 50 years after burning (Kashian et al. 2005).

Increased diversity in the vegetative community is due in part to differences in post-fire successional pathways within burn perimeters. Severity is influenced by multiple interacting forces including the composition of the pre-fire vegetation community, weather patterns, fire behavior, and topographic variables (Viereck et al. 1986, Johnson 1992, Schimmel and Granstrom 1996, Epting and Verbyla 2005, Johnstone and Chapin 2006). Post-fire vegetation establishment in the boreal forest generally follows 1 of 2 pathways: self-replacement or relay floristics (Dyrness et al. 1986, Landhäusser and Wein 1993, Johnstone and Chapin 2006). In self-replacement succession, the same species within the pre-fire community re-establish after the disturbance, whereas relay floristics succession occurs in interior Alaskan plant communities when the herbaceous (e.g., *Epilobium* spp., *Oxytropis* spp.) understory dominates immediately after fire, followed by shrub and deciduous tree establishment.

Deep soil organic horizons generally restrict germination of deciduous species in spruce-dominated boreal forests. Self-replacement by spruce is common during post-fire succession where fire intensity is low and a deep organic horizon remains (LeBarron 1939, Greene et al. 2004, Johnstone and Kasischke 2005, Johnstone and Chapin 2006). By contrast, relay floristics may take place where fire intensity is high and the organic layer is combusted to the extent that the mineral layer of the soil is exposed, allowing the germination of deciduous shrubs and trees (Johnson 1992) such as willows (*Salix* spp.), trembling aspen (*Populus tremuloides*), and paper birch (*Betula neoalaskana*).

Throughout winter moose are typically in a negative energy balance resulting in loss of body mass (Schwartz et al. 1988). The main winter browse plants in interior Alaska include twigs of several willow species, paper birch, and aspen. The abundance, availability, and quality of these browse species during winter represent, with predation, the primary limiting factors of moose populations in interior Alaska (Van Ballenberghe and Ballard 1998, Boertje et al. 2007).

Several factors mediate moose use of burned areas including the generation of deciduous vegetation, pre-fire moose population densities and movement patterns, local predation rate, snow depths and movement corridors, and patches of unburned or lightly burned cover distributed among forage areas. Peek (1974) found an increase in moose population density, specifically from increased immigration of yearlings, in the first 2 years following a large fire in northeastern Minnesota. In contrast, Gasaway et al. (1988) found no immigration into a 500 km^2 burn in interior Alaska 5 years post-burn, though moose in close proximity significantly increased their utilization of the burned areas during summer months and the pre-rut migration. Immediately following the Rosie Creek Fire near Fairbanks, Alaska in 1983, abundant regeneration of aspen, willow, and birch was present with active foraging in the area (MacCracken and Viereck 1990).

The frequency of large fire years has increased since the 1950s in interior Alaska's boreal forest, and in the last 5 decades 33% of individual fires have burned >100,000 ha (Kasischke et al. 2006). Given the extent of land burned annually and increased forage production following fires, understanding the within-fire vegetation and herbivory dynamics coupled with a greater understanding of fire behavior and scope may gain managers important insight into future moose habitat in interior Alaska.

This study focused on forage production and use patterns by moose among different fire severities within a 1994 burn outside of Delta Junction, Alaska. Whereas studies of

captive moose have demonstrated a Type-2 functional response to increased forage availability (e.g., Renecker and Hudson 1986), there is a knowledge gap pertaining to how spatial variation in forage production after disturbance affects herbivores in general (Wisdom et al. 2006), and particular to moose, regarding foraging behavior and spatial organization. To examine the effect of variable fire severity on moose habitat, we hypothesized: 1) there would be more forage biomass produced in sites that were severely burned than in those which experienced lower severity burning, and 2) moose would preferentially use areas of high fire severity.

STUDY AREA

The study area was in the flat Tanana River valley which is within the Tanana-Kuskokwim Lowlands Ecoregion (Kreig and Reger 1982, Jorgenson et al. 2001). We carried out field work within the Hajdukovich Creek Burn, approximately 40 km SE of Delta Junction, Alaska (64.0° N, 145.4° W, hereafter denoted HC94, Fig. 1). The fire burned from mid-June until September 1994 and consumed approximately 8900 ha (Michalek et al. 2000). The pre-fire vegetation was dominated by stands of black spruce with a few aspen/mixed aspen-spruce stands throughout (Michalek et al. 2000, Johnstone and Kasischke 2005). Pre-fire soil organic layer depths in black spruce stands were estimated to be >25 cm (Johnstone and Kasischke 2005). The fire event was variable in its impacts on the black spruce forest; some areas experienced complete combustion of the organic layer while other areas had only small amounts of organic duff burned off (Michalek et al.
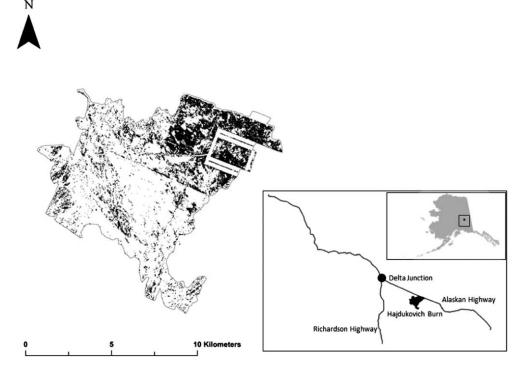

Fig. 1. Map of the 1994 Hajdukovich Creek Burn in interior Alaska. In the detail map (left), areas of high severity and low severity burning is indicated by dark and light shading, respectively.

2000). Fire severity classes were determined through post-fire satellite imagery and then field-checked for their correspondence with the depth of SOM remaining after the fire event (Michalek et al. 2000). Approximately 67% of the burn was classified as low and 33% as high severity (Michalek et al. 2000).

METHODS

We sampled 17 sites among fire severity strata (11 high and 6 low) within the HC94 perimeter which had been established in a previous study of post-fire successional pathways (Johnstone and Kasischke 2005). Sites were located using a handheld Garmin eTrex GPS unit with an approximate accuracy of 5 m (Garmin International, Inc. Olathe, KS, USA; coordinates in UTM NAD1983 Zone 6). Previous research had classified the sites as either high or low severity based on the amount of SOM remaining after the fire event (Johnstone and Kaschiske 2005, Shenoy et al. 2011). The plots were distributed along the trail system within the burn scar and accessed by snow machine and snowshoes in late March 2007. Three medium severity sites were also sampled, but were not statistically different from either high or low sites in any of the analyses, likely due to low replication; the results from these sites are not reported.

Plot Biomass Measurements

A modified browse assessment protocol was used to estimate the biomass of forage production and removal (Seaton 2002). At each site we established 30 m-diameter plots with the site GPS coordinate as the center. Random number tables were used to select distance and bearing to locate 3 plants within the accepted height range available to moose for winter browsing (0.5 – 3.0 m above ground) of each forage species (birch, aspen, and willows). Willows were identified to

species (i.e., *Salix scouleriana*, *S. bebbiana*, *S. glauca*, and *S. arbusculoides*; Simpson 1986, Collet 2004) but were grouped as *Salix* spp. in the analysis. For each plant we recorded 5 parameters: species, height, estimated number of current annual growth (CAG) twigs, percent dead material by volume, and architecture class. Plant architecture classes were defined by the percentage of the current growth (by volume) of the plant arising from any lateral branching that was due to moose browsing and were either unbrowsed (<5%), browsed (5–50%), or broomed (>50%). This classification provides a quick index for categorizing the browsing intensity on a plant throughout the course of its life (Seaton 2002).

The CAG diameter was measured with dial calipers (nearest 0.1 mm) on 10 twigs (>1 cm long) per plant for a total of 30 twigs/forage species/plot. The diameter at point of browsing (DPB) was measured if the twig was browsed by moose. Browsing by snowshoe hares was evident and we differentiated between their smooth-cut stems and the rough-edged browsing pattern of moose. If necessary, >3 plants were sampled if <30 twigs were available, until either 30 twigs or all available twigs in the plot were measured.

Stem densities were estimated within each plot using a 2 m × 30 m belt transect from a random starting point on the plot perimeter, running through the plot center. Within this transect, stems of all forage species and non-forage tree species (*Picea* spp.) above 0.5 m (typical snow depth by late winter) were counted. This sample density was then multiplied by the plot area (706.86 m²) to obtain an estimated stem count (density) within each plot.

Mass-Diameter Regressions

Twigs were collected to develop mass-diameter regression equations for all forage species (Table 1) except *Salix glauca* of

Table 1. Regression coefficients to predict dry matter (g) from twig diameter (mm) of moose browse species in the Hajdukovich Creek Burn near Delta Junction, Alaska.

Species	Intercept	Slope	MSE	n	r^2
Betula neoalaskana	0.01	5.81	0.03	20	0.89
Populus tremuloides	0.03	2.83	0.04	20	0.87
Salix bebbiana	0.01	4.38	0.04	20	0.89
Salix glauca	0.02	2.68	0.07	20	0.83
Salix scouleriana	0.02	3.11	0.22	20	0.94

which data from the Delta Junction area was provided by the Alaska Department of Fish and Game (T. Paragi, ADFG, unpublished data.). Twigs were weighed immediately upon returning to the lab or kept frozen until subsequent weighing. They were clipped and weighed at each whole diameter interval, from 2–10 mm. Samples of wet weight twigs from all diameter classes were then dried at 80 °C for 24–48 h. They were then reweighed to determine the percentage of dry mass by diameter class (Lord 2008).

The data were log transformed and a regression equation was fitted to relate dry mass to diameter (MacCracken and Van Ballenberghe 1993, Seaton 2002). We used software written in R language (R Development Core Team 2008, Version 2.1.1; code and instructions available under project 5.10 at <http://www.adfg.alaska.gov/index.cfm?adfg=librarypublications.wildliferesearch#habitat>). Dry mass calculations were then back transformed in R to obtain the original units of g of dry mass (Paragi et al. 2008).

Biomass Calculations

Biomass was calculated using the estimated dry mass from the mass-diameter regression equations. The formula used for estimating biomass production and removal was:

$$\widehat{B}_k = \sum_j \frac{M_{jk}}{m_{jk}} \sum_i \frac{N_{ijk}}{n_{ijk}} \sum_h \widehat{z}_{hijk} \quad (1)$$

where $\widehat{B}_k$ is the site estimate of removal or production biomass in grams. Twigs are denoted by h, plants by i, species by j, and the sites by k. M and m are the total and sampled plants in each plot, N and n are the total and sampled twigs, and $\widehat{z}$ denotes individual twig biomass (Seaton 2002).

Statistical Analysis

All statistical analysis was performed with SAS software, version 8.0 (SAS Institute Inc. 2002). Linear regression was used to examine the influence of SOM depth on vegetation composition (PROC REG). Differences between CAG and DPB diameters were tested using *t*-tests (PROC TTEST). One-way ANOVAS were used to test for differences in vegetation composition and moose browse consumption between severity classes (PROC GLM). We used biomass as a habitat metric, and needed to estimate it across the study area. As is often done for management purposes, with our first method we took averages of production and removal across all of our study sites and extrapolated this across the entire study area. To assess the potential effects of variable fire severity within our study area on forage production and removal, we used a second method for extrapolating our data across HC94 in which we used production and removal biomass averages from the sampled fire severity strata. We used these averages and weighted them for the final study area estimate by the proportion of high (0.67) and low (0.33) severity areas within HC94. These 2 methods allowed us to compare the resulting biomass estimates for the study area, which differed only in whether or not

they incorporated significant production and removal differences between fire severities.

Tukey's adjustment for pairwise comparisons was used to test for differences among severity classes. Values reported are means (± S.E.). All models were checked to ensure that they met basic assumptions of normality and homogeneity of variance.

RESULTS

The mean plant stem density of all principal forage species (aspen, willow, and birch) was greater ($F_{2,17}$ = 7.44, P = 0.005) across all high severity (1.80 ± 0.57 stems/m²) than low severity sites (0.67 ± 0.34 stems/m²). There was a sharp decline in the number of these stems with increasing depth of SOM. In contrast, spruce stem density ranged from 0.02–0.15 stems/m² with no difference between severity classes, and the mean number of spruce (non-forage) stems did not change with depth of SOM (Fig. 2).

Past browsing resulted in 84% of forage plants exhibiting broomed architecture, with 13% classified as browsed and 3% unbrowsed. These proportions were similar across all severity classes as well as between forage species.

An average of 190 ± 104 kg/ha of forage biomass was produced across all sites. However, high severity sites produced >3-fold more forage (225 ± 64 kg/ha) than sites of low fire severity (69 ± 48 kg/ha), and twig density was nearly 3-fold greater in high (35 twigs/m²) than low severity sites (13 twigs/m²).

Estimates of total biomass consumed/ha were larger ($F_{2,17}$ = 8.92, P = 0.002) in high (104 ± 35 kg/ha) than low severity sites (17 ± 18 kg/ha). Aspen and willow dominated the differences in consumption between fire severity classes. These species represented >95% of the forage consumed with greater ($F_{2,17}$ = 7.34, P = 0.005)
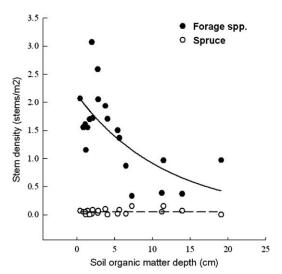

Fig. 2. Stem density of forage (aspen, birch, willow spp.) and non-forage (black spruce) plants between 0.5 – 3.0 m high, corresponding with residual SOM depth (cm) in interior Alaska. The equation for the regression on forage data is: $y = 2.13 * e^{-0.08\ x}$.

absolute biomass removal in high fire severity sites than low severity sites.

Offtake of forage relative to forage production was higher ($F_{2,17}$ = 7.46, P = 0.005) in high (46 ± <1%) than low severity sites (19 ± <1%) (Fig. 3). Across all sites, an average of 36 ± <1% of CAG was removed by moose over winter (Table 2). When we used fire severity-specific estimates of production in conjunction with the remote sensing image of burn severity to account for the area covered by each severity class, the overall estimate of forage production was 128 kg/ha. By contrast, the production estimate generated in the absence of this correction (i.e., irrespective of differences in severity) was nearly 50% higher (190 kg/ha).

DISCUSSION

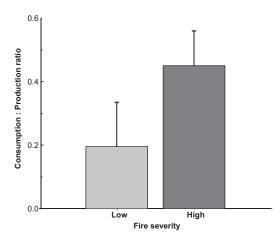Global climate change is predicted to increase the frequency and severity of large

Fig. 3. Consumption to production ratio of moose browse in the 1994 Hajdukovich Creek Burn in sites of low (n = 6) and high (n = 11) fire severity in interior Alaska; mean ± S.E.

Table 2. Estimates of biomass production and removal given high and low fire severity across the entire Hajdukovich Creek Burn in interior Alaska. Mean (S.E.) estimates represent all site data pooled. The severity-weighted estimates used the different estimates from high and low fire severity sites, coupled with burn-wide fire severity estimates derived from remote sensing, to weight the production and removal field estimates across the burn.

Severity	Production (kg/ha)	Consumption (kg/ha)	C:P
Mean	190 (104)	69 (47)	36%
Severity-weighted	128	64	49%

wildfires across the boreal landscape (Kasischke et al. 2010), creating the potential for increased moose habitat in the form of widely distributed deciduous stands. However, variable fire behavior creates a spectrum of fire severities, resulting in a range of depth in SOM that facilitates different successional pathways (Shenoy et al. 2011). We found a sharp increase in aspen stem densities where the post-fire depth of SOM

was <6 cm. A similar relationship between the SOM horizon and deciduous stem densities was found at the same sites by Johnstone and Kasischke (2005) who documented increased aspen density with increased fire severity.

The HC94 fire occurred within Game Management Unit (GMU) 20D which encompasses nearly 1.5 million ha of largely black spruce dominated boreal forest, as well as part of the Alaska Range alpine ecosystem. Much of the boreal area in GMU 20D has burned since 1979, over two-thirds between 2001 and 2004 (BLM 2005). The 2006 moose density estimate in southwestern 20D (2 moose/km^2; DuBois 2004) was among the highest in interior Alaska, exceeding that on the Tanana Flats region in GMU 20A (1.1 moose/km^2 in 2000; Seaton 2002). In addition to predator control programs in the 1980s and low snow depths in GMU 20D (DuBois 2004), it is possible that fires in this area have contributed to the increase in moose density by providing a substantial amount of high-quality winter browse. Future management decisions will need to account for the distribution of forage resources throughout the GMU, which should include an assessment of how the fire regime and individual fire behavior have shaped and will continue to influence winter habitat.

Browsing by moose in the study area was high as demonstrated by the large proportion (80%) of plants with broomed architecture throughout, regardless of severity class. Moreover, high forage offtake in interior Alaska is associated with greater mortality of browse plants (Butler and Kielland 2008) and a significant shift in plant species composition towards less preferred species, such as alder and spruce (Kielland et al. 1997, 2006). The increase in the amount of standing dead trees and evergreens suggest that browsing could accelerate fire return intervals due to increased flammability of

the vegetation after browsing. Intense browsing following wildfires may, in the short run, result in a significant numerical response by moose and high levels of consumption. However, these functional and numerical responses could cause plant mortality, reduced forage production, and ultimately have a negative feedback effect on the moose population in a relatively short period. Examples of such unsustainable growth under high moose density are clearly reflected in demographic data including low twinning rates, delayed age of first reproduction, and low body mass of short-yearlings (Boertje et al. 2007). In contrast, browsing at lower rates (when moose are at lower population density) may possibly extend the period of increased forage availability following high severity fires.

We found that stand regeneration after high severity fires produced >3x forage biomass/ha than in lightly-burned areas 14 years post-fire, underscoring the importance of using spatial information to adjust estimates of the productivity of regenerating stands. Moose responded to this heterogeneous environment by not only consuming more forage from high severity sites as predicted from the functional response, but by also consuming a much higher *proportion* of available browse. Estimates with captive animals predict that moose have the capacity to double their winter consumption rate in the observed 5-fold range of browse availability (50 – 250 kg/ha) (Renecker and Hudson 1986). In light of the functional response based on these estimates, the approximately 3-fold increase in browse production from 69 kg/ha in low severity sites to 225 kg/ha in high severity sites had the potential to increase offtake rates ~70% (from 17 to 29 kg/ha). However, we found that the actual offtake across this 3-fold increase in production resulted in a 6-fold increase in consumption or 104 kg/ha (Fig. 4). This large discrepancy between predicted and observed
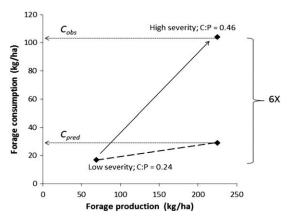

Fig. 4. Observed (C_{obs}) versus predicted (C_{pred}) magnitudes of forage consumption by moose in relation to changes in forage production in sites exhibiting low and high fire severity in the 1994 Hajdukovich Creek Burn in interior Alaska. The stippled line connects estimated increase in forage offtake as a function of forage production predicted from the functional response (Renecker and Hudson 1986).

offtake suggests that moose aggregated in areas of high browse availability and that changes in behavior at the population level (spatial organization) may supersede physiological constraints (consumption capacity) regarding browse offtake in the field.

When evaluating possible indices useful to indicate density dependent nutritional limitation in moose populations, Boertje et al. (2007) suggested that when offtake of browse is >30–35% of current production, a population may be nearing the carrying capacity of the habitat. Indeed, landscape level offtake expressed as the ratio of consumption (kg/ha) to production (kg/ha) shows a strong inverse relationship with twinning rates even at browse removal rates of <20% (Seaton et al. 2011). In our study, the average removal rate of browse across HC94 bracketed these offtake values, but we also provide evidence that there are hotspots of foraging over this large area that differ widely from the overall mean.

Currently, black spruce represents the dominant tree species of the landscape in interior Alaska (Kasischke et al. 2010). Wildfires in the interior boreal forest often cover 10,000s of ha and result in patchy regeneration of both spruce (through self-replacement succession) and deciduous (through relay floristics) stands across the landscape (Chapin et al. 2006). Over 38 million ha are in post-fire secondary succession that resulted from fires ∼25–30 years ago (BLM 2005). Since the mid-1990s-2006, almost 75 million ha have burned in interior Alaska, 63 million between 2001 and 2004 (BLM 2005). The peak of post-fire succession, from the perspective of moose habitat, can last from 10-30 years following a fire event. These fires will directly impact moose habitat by facilitating an increasingly complex vegetation community across the landscape. Coupling post-fire remote sensing data with field measurements of browse production and offtake should help managers better understand and predict the impacts of wildfire on moose habitat in boreal landscapes.

ACKNOWLEDGEMENTS

REFERENCES

BOERTJE, R. D., K. A. KELLIE, C. T. SEATON, M. A. KEECH, D. D. YOUNG, B. W. DALE, L. G. ADAMS, and A. R. ADERMAN. 2007. Ranking Alaska moose nutrition: signals to begin liberal antlerless harvests. Journal of Wildlife Management 71: 1494–1506. doi: 10.2193/2006-159.

BLM (BUREAU OF LAND MANAGEMENT-ALASKA FIRE SERVICE). 2005. Alaska Fire History, 1950–2004. Environmental Resource Institute of Michigan. http://agdc.usgs.gov/data/blm/fire/index.html <accessed October 2014>.

BUTLER, L. G., and K. KIELLAND. 2008. Acceleration of vegetation turnover and element cycling by mammalian herbivory in riparian ecosystems. Journal of Ecology 96: 136–144.

CANON, S. K., P. J. URNESS, and N. V. DEBYLE. 1987. Habitat selection, foraging behavior, and dietary nutrition of elk in burned aspen forest. Journal of Range Management 40: 433–438. doi: 10.2307/3899605.

CHAPIN III, F. S., L. A. VIERECK, P. C. ADAMS, K. VAN CLEVE, C. L. FASTIE, R. A. OTT, D. MANN, and J. F. JOHNSTONE. 2006. Successional processes in the Alaskan boreal forest. Pages 100–120 in F. S. CHAPIN III, M. W. OSWOOD, K. VAN CLEVE, L. A. VIERECK, and D. VERBYLA, editors. Alaska's Changing Boreal Forest. Oxford University Press, New York, New York, USA.

COLLET, D. M. 2004. Willows of Interior Alaska. U.S. Fish and Wildlife Service, Yukon Flats National Wildlife Refuge, Fairbanks, Alaska, USA.

DE GROOT, W. J., P. M. BOTHWELL, D. H. CARLSSON, and K. A. LOGAN. 2003. Simulating the effects of future fire regimes on western Canadian boreal forests. Journal of Vegetation Science 14: 355–364. doi: 10.1111/j.1654-1103.2003.tb02161.x.

DUBOIS, S. D. 2004. Unit 20D Moose Management Report. Alaska Department of Fish and Game, Juneau, Alaska, USA.

DYRNESS, C. T., L. A. VIERECK, and K. VAN CLEVE. 1986. Fire in taiga communities of interior Alaska. Pages 74–86 in K. VAN CLEVE, F. S. CHAPIN III, P. A. FLANAGAN, L. A. VIERECK, and

C. T. Dyrness, editors. Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function. Springer-Verlag, New York, New York, USA.

Epting, J., and D. Verbyla. 2005. Landscape-level interactions of prefire vegetation, burn severity, and postfire vegetation over a 16-year period in interior Alaska. Canadian Journal of Forest Research 35: 1367–1377. doi: 10.1139/x05-060.

Gasaway, W. C., S. D. Dubois, R. D. Boertje, D. J. Reed, and D. T. Simpson. 1988. Response of radio-collared moose to a large burn in central Alaska. Canadian Journal of Zoology 67: 325–329. doi: 10.1139/z89-047.

Greene, D. F., N. J. Bergeron, M. Roussau, and S. Gauthier. 2004. The regeneration of *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides* along a fire severity gradient. Canadian Journal of Forest Research 34: 1845–1857. doi: 10.1139/x04-059.

Hellberg, E., G. Hornberg, L. Ostlund, and O. Zachrisson. 2003. Vegetation dynamics and disturbance history in three deciduous forests in boreal Sweden. Journal of Vegetation Science 14: 267–276. doi: 10.1111/j.1654-1103.2003.tb02152.x.

Johnson, E. A. 1992. Fire and Vegetation Dynamics: Studies from the North American Boreal Forest. Cambridge University Press, Cambridge, UK.

Johnstone, J. F., and F. S. Chapin III. 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems 9: 14–31. doi: 10.1007/s10021-004-0042-x.

———, and E. S. Kasischke. 2005. Stand-level effects of soil burn severity on post-fire regeneration in a recently burned black spruce forest. Canadian Journal of Forest Research 35: 2151–2163. doi: 10.1139/x05-087.

Jorgenson, M. T., C. H. Racine, J. C. Walters, and T. E. Osterkamp. 2001. Permafrost degradation and ecological changes associated with a warming climate in central Alaska. Climatic Change 48: 551–579. doi: 10.1023/A:1005667424292.

Kashian, D. M., M. G. Turner, W. H. Romme, and C. G. Lorimer. 2005. Variability and convergence in stand structural development on a fire-dominated subalpine landscape. Ecology 86: 643–654. doi: 10.1890/03-0828.

Kasischke, E. S., T. S. Rupp, and D. Verbyla. 2006. Fire trends in the Alaskan boreal forest. Pages 285–30 *in* F. S. Chapin III, M. W. Oswood, K. Van Cleve, L. Viereck, and D. Verbyla, editors. Alaska's Changing Boreal Forest. Oxford University Press, New York, New York, USA.

———, D. L. Verbyla, T. S. Rupp, A. D. McGuire, K. A. Murphy, R. Jandt, J. L. Barnes, E. E. Hoy, P. A. Duffy, M. Calef, and M. R. Turetsky. 2010. Alaska's changing fire regime — implications for the vulnerability of its boreal forests. Canadian Journal of Forest Research 40: 1313–1324. doi: 10.1139/X10-098.

Kielland, K., J. P. Bryant, and R. W. Ruess. 1997. Moose herbivory and carbon turnover of early successional stands in interior Alaska. Oikos 80: 25–30. doi: 10.2307/3546512.

———, ———, and ———. 2006. Mammalian herbivory, ecosystem engineering, and ecological cascades in taiga forests. Pages 211–226 *in* F. S. Chapin III, M. W. Oswood, K. Van Cleve, L. Viereck, and D. Verbyla, editors. Alaska's Changing Boreal Forest. Oxford University Press, New York, New York, USA.

Kilpatrick, S. A., and D. C. Abendroth. 2000. Aspen response to prescribed fire and wild ungulate herbivory. Pages 387–394 *in* W. D. Shepperd, D. Binkley, D. L. Bartos, and T. J. Stohlgren, editors. Sustaining Aspen in Western Landscapes: Symposium Proceedings RMRS-P-18. Department of Agriculture, Forest

Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

KREIG, R. A., and R. D. REGER. 1982. Air photo analysis and summary of landform soil properties along the route of the trans-Alaska pipeline system. Geologic Report 66. Alaska Department of Natural Resources, Division of Geological and Geophysical Surveys, Juneau, Alaska, USA.

LANDHÄUSSER, S. M., and R. W. WEIN. 1993. Postfire vegetation recovery and tree establishment at the Arctic treeline: climactic-change-vegetation-response hypothesis. Journal of Ecology 81: 665–672.

LEBARRON, R. K. 1939. The role of forest fires in the reproduction of black spruce. Proceedings of the Minnesota Academy of Science 7: 11–14.

LORD, R. E. 2008. Variable fire severity in Alaska's boreal forest: implications for forage production and moose utilization patterns. M. S. Thesis, University of Alaska-Fairbanks, Fairbanks, Alaska, USA.

MACCRACKEN, J. G., and V. VAN BALLEN-BERGHE. 1993. Mass-diameter regressions for moose browse on the Copper River Delta, Alaska. Journal of Range Management 46: 302–308. doi: 10.2307/4002462.

———, and L. A. VIERECK. 1990. Browse regrowth and use by moose after fire in Interior Alaska. Northwest Science 64: 11–18.

MAIER, J. A. K., J. M. VER HOEF, A. D. MCGUIRE, R. T. BOWYER, L. SAPERSTEIN, and H. A. MAIER. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. Canadian Journal of Forest Research 35: 2233–2243. doi: 10.1139/x05-123.

MICHALEK, J. L., N. H. F. FRENCH, E. S. KASISCHKE, R. D. JOHNSON, and J. E. COLWELL. 2000. Using Landsat TM data to estimate carbon release from burned biomass in an Alaskan spruce forest complex. International Journal of Remote Sensing 21: 323–338. doi: 10.1080/014311600210858.

PARAGI, T. F., C. T. SEATON, and K. A. KELLIE. 2008. Identifying and evaluating techniques for wildlife habitat management in interior Alaska: moose range assessment. Federal Aid Wildlife Restoration, Project 5.10. Final Research Technical Report, Grants W-33-4 through W-33-7. Alaska Department of Fish and Game, Juneau, Alaska, USA.

PASTOR, J., Y. COHEN, and R. MOEN. 1999. Generation of spatial patterns in boreal forest landscapes. Ecosystems 2: 439–450. doi: 10.1007/s100219900092.

PEEK, J. M. 1974. Initial response of moose to a forest fire in northeastern Minnesota. American Midland Naturalist 91: 435–438. doi: 10.2307/2424334.

RENECKER, L. A., and R. J. HUDSON. 1986. Seasonal foraging rates of free-ranging moose. Journal of Wildlife Management 50: 143–147. doi: 10.2307/3801504.

RIGGS, R. A., and J. M. PEEK. 1980. Mountain sheep habitat-use patterns related to post-fire succession. Journal of Wildlife Management 44: 933–938. doi: 10.2307/3808329.

SCHIMMEL, J., and A. GRANSTROM. 1996. Fire Severity and Vegetation Response in the Boreal Swedish Forest. Ecology 77: 1436–1450. doi: 10.2307/2265541.

SCHWARTZ, C. C., M. E. HUBBERT, and A. W. FRANZMANN. 1988. Energy requirements of adult moose for winter maintenance. Journal of Wildlife Management 52: 26–33. doi: 10.2307/3801052.

SEATON, C. T. 2002. Winter foraging ecology of moose in the Tanana Flats and Alaska Range Foothills. M.S. Thesis, University of Alaska-Fairbanks, Fairbanks, Alaska, USA.

———, T. F. PARAGI, R. D. BOERTJE, K. KIELLAND, S. DUBOIS, and C. L. FLEENER. 2011. Browse biomass removal and nutritional condition of moose, Alces alces. Wildlife Biology 17: 55–66. doi: 10.2981/10-010.

SHENOY, A., J. JOHNSTONE, E. KASISCHKE, and K. KIELLAND. 2011. Persistent effects of fire severity on early successional forests in interior Alaska. Forest Ecology and Management 261: 381–390. doi: 10.1016/j.foreco.2010.10.021.

SIMPSON, D. T. 1986. Key for the Identification of Salix in Interior Alaska. Unpublished Manual, 9 pp.

VAN BALLENBERGHE, V., and W. B. BALLARD. 1998. Population dynamics. Pages 223–245 in A. W. FRANZMANN and C. C. SCHWARTZ, editors. Ecology and Management of the North American Moose. Smithsonian Institute Press, New York, New York, USA.

VIERECK, L. A., K. VAN CLEVE, and C. T. DYRNESS. 1986. Forest ecosystem distribution in the taiga environment. Pages 22–43 in K. VAN CLEVE, F. S. CHAPIN III, P. A. FLANAGAN, L. A. VIERECK, and C. T. DYRNESS, editors. Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function. Springer-Verlag, New York, New York, USA.

WEIXELMAN, D. A., R. T. BOWYER, and V. VAN BALLENBERGHE. 1998. Diet selection by Alaskan moose during winter: effects of fire and forest succession. Alces 34: 213–238.

WISDOM, M. J., M. VAVRA, J. M. BOYD, M. A. HEMSTROM, A. A. AGER, and B. K. JOHNSON. 2006. Understanding ungulate herbivory-episodic disturbance effects on vegetation dynamics: knowledge gaps and management needs. Wildlife Society Bulletin 34: 283–292. doi: 10.2193/0091-7648(2006)34[283:UUHDEO]2.0.CO;2.