

Boreal Fire Effects on Subsistence Resources in Alaska and Adjacent Canada

Joanna L. Nelson,^{1,*} Erika S. Zavaleta,¹ and F. Stuart Chapin III²

¹*Environmental Studies Department, University of California, 1156 High Street, Santa Cruz, California 95064, USA;* ²*Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA*

ABSTRACT

Rural communities in the northern boreal forest depend on a suite of wild species for subsistence, including large game animals, furbearers, fish, and plants. Fire is one of the primary ecological disturbances and determinants of landscape pattern in the northern boreal forest. We review responses of key boreal subsistence species to variation and change in post-fire stand age and other characteristics. Available data for 17 species indicate highly varied post-fire habitat requirements. Mosaics of differing stand ages generated by fire could therefore be most effective in supplying a suite of subsistence species to hunting-and-gathering communities. Recent and projected increases in frequency of large-fire years might produce a more

homogeneous landscape dominated by younger stand ages. Increases in fire suppression around communities might also produce a more homogeneous landscape, but dominated by older stand ages. Neither of these scenarios provides mixed habitats for a diverse suite of subsistence species. We suggest that one aspect of the complex suite of human–fire interactions is an understanding of wildlife and plant species' response to fire in a subsistence region, in an effort to sustain ecosystem services critical to human well-being.

Key words: boreal forest; fire; subsistence; patch dynamics; ecosystem services; caribou; moose.

INTRODUCTION

Disturbance-generated landscape heterogeneity shapes ecosystem dynamics and processes, including organism movements and the population dynamics of wild species (Pickett and White 1985; Turner 1989). Wildfire is one of the primary ecological disturbances influencing landscape pattern and patch size in the North American northern boreal forest (Viereck 1973; Bonan and Shugart 1989; Kasischke and others 2002). Fire is therefore an important determinant of many ecosystem goods and services, ranging from air quality to

habitat renewal and availability of game species. Many indigenous communities in the boreal forest of North America depend on these flows because of continued, widespread reliance on hunting and gathering for both nutrition and the maintenance of cultural identity (Fall 1990; Krupnik and Jolly 2002). Communities in boreal Alaska depend on more than 50 wild species for subsistence, including large game animals, furbearers, fish, and edible and medicinal plants (Scott and others 2001) (Figure 1). Fire-related changes in the community composition and structure of landscapes that supply these species are therefore likely to strongly affect subsistence opportunities and associated cultural continuity represented by hunting, fishing, trapping, and gathering of wild foods.

Received 14 November 2006; accepted 20 November 2007; published online 3 January 2008.

*Corresponding author; e-mail: jolektra@ucsc.edu

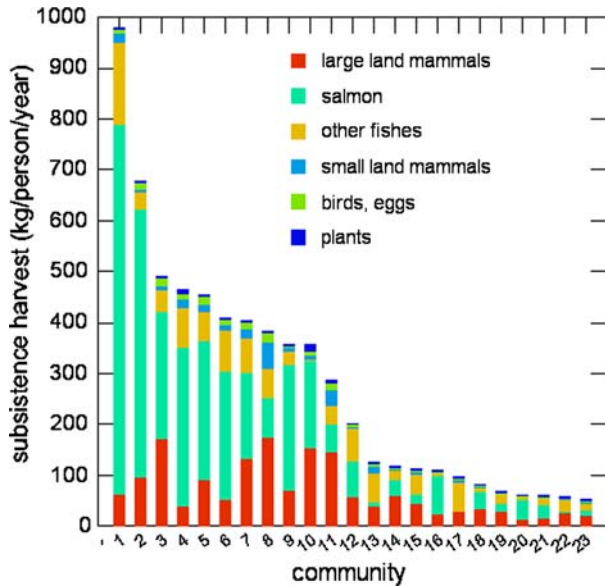


Figure 1. Composition of annual subsistence harvest for 23 rural communities in interior Alaska. *Source:* Alaska Department of Fish and Game Subsistence Division surveys conducted 1982–1990 (values may have changed considerably in the intervening period). *Communities:* 1-Tanana, 2-Hughes, 3-Huslia, 4-Minto, 5-Ft. Yukon, 6-Allakaket/Alatna, 7-Grayling, 8-Anvik, 9-Galena, 10-Nikolai, 11-Holy Cross, 12-Shageluk, 13-Northway, 14-Bettles/Evansville, 15-Tanacross, 16-McKinley Park, 17-Tetlin, 18-McGrath, 19-Tok, 20-Anderson, 21-Healy, 22-Chisana, 23-Dot Lake. There is over a 10-fold difference in the amount of subsistence resources used by different villages.

North American and Australian definitions of landscape ecology focus on causes and consequences of spatial pattern at variable spatial scales defined by the organism or process of interest (Turner 2005). In this article, we focus on the configuration of forest stands of different ages, where stand ages are determined by time since last fire, relative to the habitat requirements of animals, plants, and fish important to subsistence communities. We define the landscape in the context of subsistence as an area of radius approximately 50–150 km, set by the furthest distance rural subsistence hunters routinely travel to hunt, fish, trap and gather (Chapin and others 2004; M. Bifelt and J. L. Nelson, unpublished interviews).

Fire regimes in boreal forests are responding to anthropogenic climate change as well as to human ignitions and suppression activity. Air temperature has increased by approximately 2°C since 1950, and surface moisture has declined throughout much of the circumboreal zone, particularly in Alaska and western Canada (Serreze and others

2000). This warming correlates with a doubling of annual area burned in the boreal forest of western North America since 1965 (Murphy and others 2000). In Alaska the shift in the fire regime began in the mid-1980s, with 70% greater annual area burned for the period of 1985–2006 than from 1950 to 1984 (Kasischke and others 2006). A parallel shift in seasonality toward more late-season burning increased the severity of the more recent fires (Kasischke and others 2006; Kasischke and Turetsky 2006). In western Canada, fires now burn more than 95% of the area within a burn perimeter (Eberhart and Woodard 1987; Kafka and others 2001), converting landscapes of multiple stand ages to early successional vegetation of a single predominant stand age. Projections suggest that air temperature will increase more rapidly during the 21st century (0.4–0.7°C decade⁻¹, up from 0.4°C decade⁻¹) (ACIA 2005). Fire scenarios in a warming climate suggest a future with more frequent, larger fires, and landscapes with a more homogeneous distribution of stand ages, more early successional deciduous forest, and less mature spruce forest (Stocks and others 2000; Flannigan and others 2005) (Table 1).

Fire alters habitat for most subsistence species harvested by rural communities. Post-fire vegetational succession can follow multiple trajectories, but some pathways recur more frequently than others (Viereck 1970). Succession ranges from self-replacement, in which the dominant tree species quickly resumes dominance (more common in extremely cold or dry soil conditions), to relay floristics, in which plant species show sequential patterns of dominance (Chapin and others 2006). In boreal forest relay floristics, succession resets with grasses, sedges, forbs, and resprouting shrubs (Viereck 1973), becomes increasingly shrub-dominated, then dominated by deciduous tree species and eventually reverts to late-successional deciduous or coniferous forest (Foote 1983). Although every fire event produces unique fine-scale patterning and trajectory of change, the successional dynamics described in the literature and summarized above provide a useful starting point for considering fire-directed landscape pattern. Changes in fire frequency, severity, and/or extent will likely impact landscape-level vegetation patterns (Rupp and others 2002). We explore how a mosaic of post-fire patches in different stages of vegetational succession may contribute to the provision of subsistence goods and services to rural human communities in the boreal forest. In this article, we review fire effects on plant and animal species important to subsistence and explore how direc-

Table 1. Summary Effects of Fire on Subsistence Resources in the North American Boreal Forest

Organism	Summary
Moose	Increased densities 5–26 (especially 12–26) years post-fire; no evidence of moose declines immediately post-fire. Main mechanism appears to be browse availability
Caribou	Winter use declines for ~60 (range 20–150) years post-fire due largely to forage (lichen) declines. Possible that stands >150 years old lose habitat value because lichens decline
Lynx	Stands 15–30 post-fire generally produce good habitat for lynx and their prey of snowshoe hares in interior Alaska. Denning habitat may differ from foraging habitat
Marten	Higher densities in 15-year post-burn sites than in 25-year or mature forest sites, but only non-breeding individuals found in the 15-year site. Suggests need for both mature and burned sites
Grizzly bear and black bear	Consume berries and moose calves, both found in higher densities in early to mid-successional stages. Bears are documented foraging in areas 5–40 years post-fire, and in Canada, selecting dens in mature aspen or spruce forest, suggesting mixed habitat needs
Grouse	Little-studied; generally, sharp-tailed grouse use recent burns, ruffed grouse prefer intermediate-aged stands, and spruce grouse prefer mature forest
Ptarmigan	Little-studied; willow ptarmigan may benefit from recent fire due to increase in shrubby habitat; willow buds (winter food)
Salmon, whitefish, and blackfish	Few data exist
Blueberry and Lingonberry (genus <i>Vaccinium</i>)	Berry yield may peak at 3–30 years after light-moderate fires, depending on light availability (openness of forest canopy), depth of organic mat burned, and pre-fire population from which to resprout

tional changes in wildfire regimes in the Alaskan and northern Canadian boreal forests could affect subsistence resource availability. We build on previous reviews indicating that different post-fire stand ages favor different wildlife species, each with specialized and often highly seasonal habitat requirements (Viereck and Schandelmeier 1980; Fisher and Wilkinson 2005). The co-occurrence of a full suite of subsistence species within distances accessible to permanent communities of hunters and gatherers should therefore depend on a sufficiently diverse post-fire landscape mosaic.

Although most research on wildlife responses to fire has focused on stand-level effects, we extend these results to the landscape scale, where possible, to assess the potential impact of changes in fire regime and management on local subsistence opportunities, paying particular attention to temporal trajectories of change.

METHODS

We selected study species based on detailed subsistence use surveys conducted by the Subsistence Division of the Alaska Department of Fish and Game (<http://www.subsistence.adfg.state.ak.us/>) and on conversations with anthropologists, residents, and managers of the boreal forest region of Alaska. We focused on terrestrial and freshwater

species resident in the boreal forest that are most frequently used, excluding migratory birds. We searched Web of Science, Biosis, and for aquatic species, Aquatic Sciences and Fisheries Abstracts with the terms “*species* AND boreal AND fire” where *species* was “moose”, “caribou”, “salmon”, “whitefish”, “blackfish”, “bear”, “wolf”, “furbearer”, “marten”, “fisher”, “lynx”, “wolf”, “hare”, “beaver”, “muskrat”, “grouse”, “ptarmigan”, or “berries”. To capture material from unpublished reports and agency documents (“gray” literature), we searched annotated bibliographies (Magoun 1991; Saperstein and Joly 2001), unpublished reports (Foote 1983; Johnson and others 1995), and the Fire Effects Information System of the US Forest Service (<http://www.fs.fed.us/database/feis/>) for both data and citations, then repeated this cycle for all relevant articles located (both published and “gray”) until we stopped discovering new references.

FINDINGS

Most available literature focuses on the effects of time since fire. Where possible, we also report effects of fire size, severity, and seasonality. Scant literature exists about many subsistence resources including large carnivores such as bears and wolves; grouse and ptarmigan; and salmon,

whitefish, and blackfish. However, certain key subsistence species have been studied in sufficient detail to support qualitative assessments of ways in which changing fire regimes could affect their availability.

Moose

Moose (*Alces alces*) are the main terrestrial subsistence species harvested in interior Alaska (Figure 2), contributing as much as 165 kg person⁻¹ y⁻¹ to the diet (median 39 kg person⁻¹ y⁻¹) (Scott and others 2001). Moose population increases have been observed in early successional forests (Spencer and Hakala 1964; Peek 1974; Loranger and others 1991), whereas mature conifer forest supports few moose (Scotter 1971a; Cederlund and Okarma 1988). Relatively recently burned areas (one to a few decades old) are described as more favorable for moose: those with resprouting and reseeded deciduous hardwoods including aspen, birch, willow, and in some cases, cottonwood that serve as winter forage (Leopold and Darling 1953; Spencer and Hakala 1964; MacCracken and Viereck 1990; Collins and Helm 1997). Protein and mineral concentrations of browse species decreased with time post-fire in one interior Alaskan study (MacCracken and Viereck 1990), suggesting that recent fire can enhance forage quality as well as availability. A great deal of research on fire effects on moose densities has been conducted in south-central Alaska, with less work in the boreal forest region of interior Alaska where large fires are more frequent (a visual assessment of the fire-scar map of Alaska 1950–2006 shows the vast majority of large fires (greater than 450 ha or 1000 acres) in interior Alaska between the Brooks Range and the Alaska Range (Alaska Geospatial Data Center)).

Time since fire for optimal moose habitat and forage are most frequently reported in the range of 10–26 years, with subsequent declines in population density as stands mature (Figure 3A) (Spencer and Hakala 1964; Kelsall and others 1977; Gasaway and others 1989; Loranger and others 1991; Maier and others 2005). However, one source suggests that 60–70 years or longer are sometimes needed to produce favorable conditions (Spencer and Hakala 1964). Fire severity can strongly affect the time course of moose response. High-severity fires that burn the majority of the organic soil layer likely kill belowground vegetation and prevent sapling and shrub resprouting (although the bare mineral soil exposed is favorable for seeding of deciduous shrubs and trees (Johnstone and Kasischke 2005; Johnstone and Chapin 2006), delaying in turn use

by moose. However, light fires can produce forage within months. MacCracken and Viereck (1990) reported abundant browse resprouting within 2 months after a 1983 fire in forests of quaking aspen (*Populus tremuloides*), paper birch (*Betula neoalaskana*), and white and black spruce (*Picea glauca* and *P. mariana*) in interior Alaska. Moose foraged in the burned area the winter after the fire. Moose browse was available during and immediately after a wildfire on the Tanana Flats, Alaska, in unburned islands within the burn perimeter and from resprouting in lightly burned areas (Gasaway and Dubois 1985). Moose increasingly used the lightly burned areas for 4 years post-fire (Gasaway and Dubois 1985). In contrast, moderately and severely burned stands (~75% of the 1980 burn area) had little moose browse 1–5 years later (Gasaway and others 1989).

Spatial and seasonal variability in moose density in Alaska reflects several factors, including post-fire forage quality, landscape heterogeneity, and historical dynamics such as ease of travel, access to forage, predator avoidance, game management, human land use, riparian-area dynamics of flooding, erosion, and ice scour, and winter conditions such as snow depth, ice, temperatures and wind (Spencer and Hakala 1964). Physical barriers, such as downed trees, may hinder moose from gaining access to certain areas post-fire (MacCracken and Viereck 1990). Moose also have traditional travel routes and are unlikely to use a burned area if they have no pre-fire contact with that area (Gasaway and others 1989). In the Kenai Peninsula, Alaska, moose did not distinguish between post-fire stands of different ages, but their diet selectivity declined with increasing distance from cover, indicating that predation risk played a role in foraging dynamics (Weixelman and others 1998). Uplands and lowlands may also provide different conditions for moose: in riparian areas ice scour and other riverine processes provide vegetation renewal and desirable forage, whereas uplands rely on fire to renew browse (Collins and Helm 1997). One recent study examined female moose density in interior Alaska in relation to vegetation type, topography, occurrence and timing of fire, distance to rivers and towns, and landscape metrics (Maier and others 2005). Their analysis revealed that moose density was highest in areas that had burned 11–30 years ago, with positive associations at all spatial scales examined and significant relationships at 15- and 23-km² scales. However, the densest populations occurred close to towns, at moderate elevations, and close to river corridors. Another study found river riparian corridors more important than fire

history in explaining the variation in aerially surveyed November moose densities (Jandt 1992). In relation to subsistence, the difference between disturbance in uplands and lowlands (fire and ice scour, respectively) can lead to different perceptions of whether moose densities do in fact increase after fire: hunters who travel river corridors, in the fall moose hunting season, would be unlikely to perceive changes in upland moose populations. Eleven to thirty years after fire might seem a short interval for a land manager concerned with maintaining moose in a forest with a 30–200-year fire return interval; on the other hand, it might not, because managers' long-term plans are often on the order of 15–20 years (Zavaleta, unpublished interviews). For hunters who are fixed in location by modern village infrastructure, 15–20 years represents a generation before they or their children have high-likelihood of moose-hunting success, so recent increases in fire extent are of great concern to rural communities (Huntington and others 2006).

Caribou

Caribou (*Rangifer tarandus*) is the only large herbivore besides moose harvested by most boreal forest subsistence communities, contributing a maximum of 22 kg person⁻¹ y⁻¹ (median 3.5 kg person⁻¹ y⁻¹) (Scott and others 2001) (Figure 2), an order of magnitude less harvested meat than moose. In

contrast to moose, caribou rely on winter forage in spruce-lichen forests that are typically at least 80 years old (Klein 1982; Schaefer and Pruitt 1991; Thomas and others 1996; Arseneault and others 1997; Joly and others 2003) (Figure 3B). Early researchers considered fire responsible for caribou declines (Leopold and Darling 1953; Lutz 1956). Researchers since the late 1960s typically conclude that fire is not responsible for caribou declines in North America, but agree that caribou appear to avoid burned areas for many decades or longer (Skoog 1968; Scotter 1971a; Johnson and Rowe 1975; Kelsall and others 1977; Miller 1980; Joly and others 2003; Rupp and others 2006). On time scales of centuries, fire could enhance the maintenance of lichen communities and nutritional quality of forage in boreal forest (Klein 1982). However, fire return times in boreal interior Alaska are typically 30–200 years (Yarie 1981; Viereck and others 1986; Kasischke and others 2002), so benefits on multi-century time scales are not realized in most areas.

Forage availability appears to be the key mechanism controlling fire effects on caribou density (Klein 1982; Joly and others 2003). The fruticose lichens (*Cladina* or *Cladonia* spp.) preferred by caribou (Schaefer and Pruitt 1991; Thomas and others 1996) are very susceptible to fire and recover extremely slowly from it (Scotter 1971b; Viereck and Schandelmeier 1980). However, rate of lichen

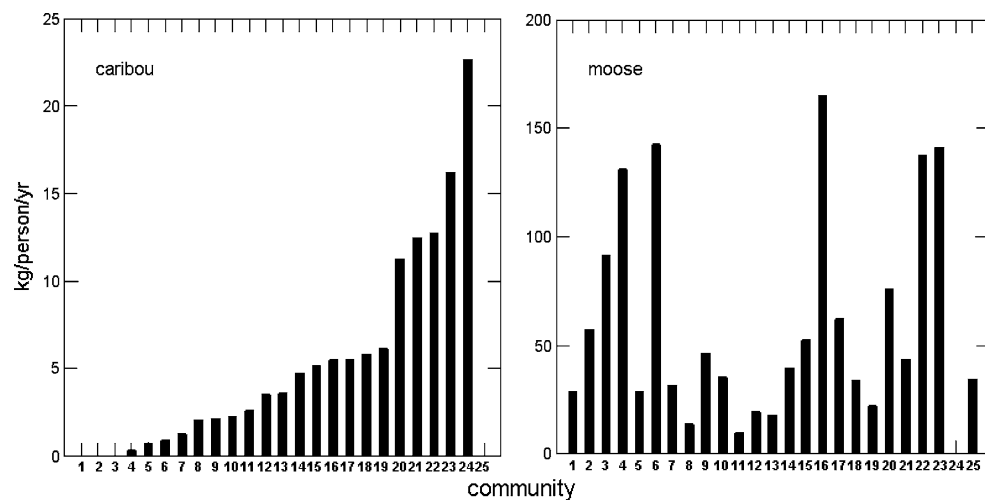


Figure 2. Annual harvest of moose and caribou by 24 rural communities in interior Alaska. Caribou data are shown in the left panel and moose data on the right; please note difference in scale on the y-axis. *Source:* Alaska Department of Fish and Game Subsistence Division surveys conducted 1982–1990 (values may have changed considerably in the intervening period). *Communities:* 1-Ruby City, 2-Shageluk, 3-Hughes, 4-Grayling, 5-Tetlin, 6-Holy Cross, 7-McGrath, 8-Healy, 9-Allakaket/Alatna, 10-Nulato, 11-Anderson, 12-McKinley Park, 13-Dot Lake, 14-Tanacross, 15-Tanana, 16-Anvik, 17-Galena, 18-Northway, 19-Tok, 20-Ft. Yukon, 21-Bettles/Evansville, 22-Nikolai, 23-Huslia, 24-Chisana, 25-Minto (no caribou data available).

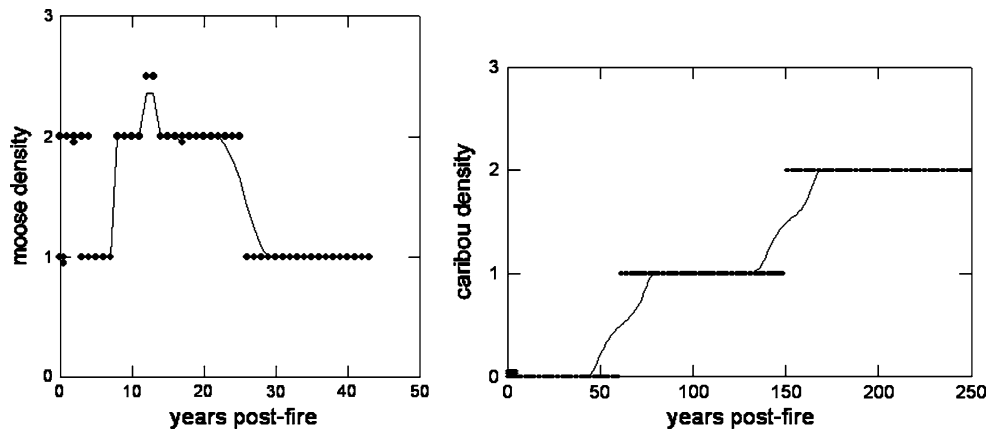


Figure 3. Effects of time since fire on (A) moose density ($n = 6$ studies) and (B) caribou density ($n = 4$ studies). Categorical density values: 0-absence of the species from study sites; 1-no change from pre-fire density/presence with no indication of change from pre-fire density; 2-increased density relative to pre-fire density; 2.5-peak above other years with density greater than pre-fire values. Identical data points provided by more than one study are indicated with two vertically aligned dots in the figures. Points are fitted with LOWESS curves (tension = 0.3), which interpolate y-values from weighted averages of nearby reported y-values (Systat 10.2, Systat Software Inc.).

recovery depends on the characteristics of a fire. Within burns in Sweden, there was no lichen recovery 140 years after a severe wildfire, but recovery took only 20 years after a light, controlled burn (Skuncke 1969). Rate of lichen recovery could also vary along regional climate gradients. Slow recovery rates reported on the Seward Peninsula, Alaska and rapid rates in Newfoundland (Viereck and Schandelmeier 1980) could reflect the warmer climate in the latter site. Similarly, caribou lichen biomass (*Cladina* spp. and *Cetraria nivalis*) recovered and stabilized 61–80 years post-fire in the westernmost study area but only 41–60 years post-fire in the easternmost study area in one northern Canada study (Thomas and others 1996). The precise duration of reduced caribou use of burned areas will therefore depend on fire characteristics as well as landscape, climate, and previous fire history at both regional and more local scales. Factors other than forage availability may also affect caribou densities in post-fire patches: unfavorable snow conditions and downed trees have been suggested as detrimental to winter travel in burns (Schaefer and Pruitt 1991; Thomas and others 1996). One northern Canada study found that caribou made little use of forests younger than 60 years even when sufficient forage was present (Thomas and others 1996).

Furbearers: Wolf, Lynx, Hare, and Marten

These four species are harvested primarily for their pelts, either for household use in winter clothing or for cash income. We report their use on the scale of

the community, because pelts are not divided and shared in the same way as edible harvests. Available ecological data suggest that all of these species benefit from relatively young to intermediate-aged burns (6–30+ years post-fire) for at least some of their habitat needs and life history stages.

Few data exist on fire effects on wolves (*Canis lupus*), although existing studies suggest that moose and caribou densities can both affect wolf use of post-fire areas. Wolf packs in the Kenai Peninsula, Alaska, used an area encompassing burns 9+ years old and 30+ years old and occurred in similar densities in each burn (Peterson and others 1984; Schwartz and Franzmann 1989). Wolves used burned areas more than expected during and 1 year after a northwest Alaskan taiga forest fire, but use dropped during the subsequent two winters before returning to pre-fire levels (Ballard and others 2000); the observed changes in wolf distribution were attributed to shifts in caribou distribution. Subsistence wolf catch is reported as an average of 8 individuals/community⁻¹ y⁻¹ (Scott and others 2001).

Lynx (*Lynx canadensis*) in Alaska and Canada prey primarily on snowshoe hares (*Lepus americanus*) (Nellis and others 1972; Brand and others 1976; Paragi and others 1997; O'Donoghue and others 1998). Both species exhibit preferences for mid-successional regenerating forest (Mowat and Slough 2003; Fisher and Wilkinson 2005), with hares selecting for denser growth (O'Donoghue and others 1998) and avoiding open, recently burned areas (<1–3 years) until post-burn regeneration can provide sufficient cover (Grange 1932;

Keith and Surrendi 1971; Pietz and Tester 1983; Litvaitis and others 1985), suggesting that burns create high-quality habitat after 15–30 years. Trapper accounts from interior Alaska suggest that lynx can re-occupy burns as early as 5 years post-fire and remain abundant in burns up to 50 years old (Stephenson 1984). Lynx denning habitat, however, may differ from foraging habitats and may occur under deadfall debris in burns, in willow shrub thickets, or in mature forest (Koehler 1990; Slough 1999). Subsistence lynx catch is a mean of 29 individuals/community⁻¹ y⁻¹, and snowshoe hare is a mean catch of 1412 individuals/community⁻¹ y⁻¹ for pelts, and 4 kg/person⁻¹ y⁻¹ as edible meat (Scott and others 2001).

Early researchers identified mature conifer stands as optimal for marten (*Martes americana*) and fisher (*Martes pennanti*) and recommended fire suppression to maintain populations of these furbearers (Lutz 1956). Further evidence emphasizes martens' and fishers' dependence on late-successional, coniferous forest for foraging, resting, and reproduction (Harris 1984; Arthur and others 1989; Buskirk 1994; Buskirk and Powell 1994). Both species need closed canopy tree cover and complex physical structure, usually of downed logs and branches, at ground level (Buskirk 1994). However, some evidence indicates that in the northern boreal forest marten can utilize more open, younger forests after wildfire (Magoun and Vernam 1986b; Latour and others 1994; Paragi and others 1996). Paragi and others (1996) found that marten abundance and activity in interior Alaska were greater in an area 6–9 years post-fire than in areas either 25–28 years or 100–115 years post-fire, although use of the recent 6–9 year-old burn was primarily by non-breeding juveniles. In another interior Alaskan site, marten hunted and rested within a 7–9 year-old burn (Magoun and Vernam 1986b). Martens may also use different stand ages at particular life history stages or use burns as suboptimal habitat (Fisher and Wilkinson 2005). Interviews with Alaskan trappers indicated that fire is generally favorable for marten (Stephenson 1984). Light to moderate fire might maintain a mosaic of habitats that marten utilize for travel, cover (under deadfall), foraging, and denning (Koehler and Hornocker 1977; Magoun and Vernam 1986a). Habitat preferences also reflect prey densities of microtine rodents (Cowan and Mackay 1950; Lensink and others 1955; Martin 1994). Yellow-cheeked voles (*Microtus xanthognathus*) and red-backed voles (*Clethrionomys rutilus*) in interior Alaska colonize and experience population increases in recently burned areas (West 1982; Le-

hmkuhl 2000). Marten catch is reported as an average of 636 individuals/community⁻¹ y⁻¹ (Scott and others 2001). No data were found on fisher use of burned habitats in the northern boreal forest.

Beaver and Muskrat

Although beaver (*Castor canadensis*) and muskrat (*Ondatra zibethicus*) are primarily trapped for their pelts, we describe fire effects on their habitats separately from other furbearers because these organisms are aquatic. Beaver and muskrat are also eaten, although not as frequently as in past decades (M. Bifelt and J. Nelson, unpublished data). Annual beaver consumption varies considerably among boreal forest communities (range 0–50 kg person⁻¹ y⁻¹, mean 6.8 kg person⁻¹ y⁻¹). Muskrat catch is not recorded in the subsistence database. Fire is thought to benefit maintenance of wetland and aquatic edge habitat for beaver and muskrat in boreal forest (Kelsall and others 1977; Viereck and Schandelmeier 1980), but few studies exist. Beaver depend primarily on deciduous trees for food and necessary building supplies (Kelsall and others 1977). Two Canadian studies concluded that fire benefits beaver habitat where aspens are an early successional, disturbance-reliant species (Slough and Sadleir 1977; Barnes and Mallik 2001). Kelsall and others (1977) suggest that beaver are virtually absent from areas where coniferous forest dominates. However, in a study from Elk Island National Park, Canada, beaver lodge occupancy declined over a 12-year period of prescribed fires and did not return to pre-fire levels (Hood and others 2007). Muskrat data comes primarily from the southeastern US, where marshes are burned to promote muskrat habitat (Errington 1963). In one Manitoba, Canada study, summer marsh burning increased autumn muskrat populations (Ward 1968), and Athabascans in eastern Alaska traditionally burned lake edges to improve muskrat habitat (Natcher 2004). Flooding, erosion, and ice scour could also be important disturbances in the aquatic habitats of beaver and muskrat, as reported for lowland moose, but we found no studies available.

Bears

Bears make up a relatively small part of the subsistence harvest of most interior Alaska communities, with a mean black bear (*Ursus americanus*) harvest of 2.3 kg person⁻¹ y⁻¹ and smaller harvests of grizzly (brown) bears (*Ursus arctos*). However, for individual households a single bear harvested can make a substantial contribution to food supplies, can be shared widely among neighbors, and rep-

resents an important cultural resource (Scott and others 2001). Available studies show that fire indirectly benefits bears by increasing foraging opportunities, due to benefits to moose density, increased moose calf productivity, and greater berry yield (genera *Vaccinium* and *Shepherdia*) (Schwartz and Franzmann 1989, 1990; Hamer 1996; Fisher and Wilkinson 2005). In Yellowstone National Park, Wyoming, large wildfires in 1988 caused elk mortality, and grizzly bears scavenged the elk carcasses (Blanchard and Knight 1990). On the Kenai Peninsula, Alaska, growth and reproduction rates of black bears were greater in a 13–18 year-old burn than in a 35–40 year-old burn (Schwartz and Franzmann 1990). Fire may also improve denning habitat; in Alberta, Canada, black bears selected den sites in mature aspen (*Populus* spp.) and spruce (*Picea* spp.) stands and avoided later successional muskeg sites (Tietje and Ruff 1980).

Grouse and Ptarmigan

Upland game birds, including grouse and ptarmigan species, make up a small (typically <3 kg person⁻¹ y⁻¹) part of the food harvests in interior Alaska. Long-term fire effects on these birds are mediated by vegetation changes (Viereck and Schandelmeier 1980). Research in Alaska and Canada suggests that ruffed grouse, sharp-tailed grouse and spruce grouse each prefer different successional stages (Kelsall and others 1977). Sharp-tailed grouse (*Tympanuchus phasianellus*) thrive in fire-prone areas (Viereck and Schandelmeier 1980). Periodic fires are beneficial to ruffed grouse (*Bonasa umbellus*) populations (Weeden 1965; Sharp 1971), which prefer early successional aspen forest (Viereck and Schandelmeier 1980). Limited evidence suggests that spruce grouse (*Falcapenniss canadensis*) could prefer later successional stages (Ellison 1975; Kelsall and others 1977). Although very little research has been done on other upland bird species, fires that replace mature forest with shrubby growth probably benefit willow ptarmigan (*Lagopus lagopus*) through their forage of willow buds (Weeden 1965; Viereck and Dyrness 1979).

Salmon, Blackfish, and Whitefish

Fish are the staple of interior Alaska subsistence diets, comprising 30 to more than 90% of total subsistence harvests (mean 61%) across 22 villages surveyed in 1982–1990 (Scott and others 2001) (Figure 1). Salmon alone make up 41% by weight (SD 24%) of subsistence harvests, with a mean

harvest of 149 kg person⁻¹ y⁻¹. Important species include king, coho and chum salmon (*Oncorhynchus tshawytscha*, *O. kisutch*, and *O. keta*, respectively), Alaska blackfish (*Dallia pectoralis*), broad whitefish (*Coregonus nasus*) and humpbacked whitefish (*Coregonus oidschian*).

Fire may affect aquatic environments through terrestrial vegetation removal; increased erosion or ash flow into streams and lakes; altered patterns of sedimentation, turbidity, and nutrient dynamics; reductions in dissolved oxygen via nutrient enrichment; leaf litter input; buildup of woody debris and other physical habitat alteration; and increased solar radiation due to canopy removal (Kelsall and others 1977; Minshall and others 1989; Gresswell 1999; Howell 2001). Fish mortality as a result of wildfire has been reported, but the mechanisms and magnitude of effects are generally unclear (Hakala and others 1971; Minshall and others 1989; Gresswell 1999).

Salmon species and whitefish species typically spawn on gravel beds (Alt 1994; Delaney 1994) and may be impacted by increased erosion and sedimentation. Salmonids are sensitive to changes in water temperature (McCullough and others 2001). Even after highly severe fires, however, local extirpation of fishes is patchy and recolonization is rapid (Hakala and others 1971; Rieman and Clayton 1997; Gresswell 1999). A study of lakes in Alberta, Canada compared burned and logged catchments to undisturbed reference areas. Researchers found that although fires could potentially cause nutrient enrichment or altered hydrology, the level of disturbance in a catchment explained less than three percent of the variation in fish assemblage structure (Tonn and others 2003). In another Alberta lake study, the only observed difference after burning was a decrease in small northern pike (Tonn and others 2004). Several researchers have called for long-term studies of fire effects on boreal aquatic environments (Lotspeich and others 1970; Gresswell 1999; Adams and others 2004).

Berries

Edible berries are the principal plant food harvested for subsistence in the boreal forest. They make up a small proportion of overall subsistence harvests by weight (mean 2.6 kg person⁻¹ y⁻¹), but their gathering in summer is an important cultural activity across generations. Edible berries in the boreal forest of Alaska and adjacent Canada include at least six species; blueberry (*Vaccinium uliginosum*) and lingonberry (also known as low-bush cran-

berry, *Vaccinium vitis-idaea*) are the best studied and most important species to subsistence diets in interior Alaska. Most data, however, deal with fire effects on vegetative plant parts rather than on fruit availability; the two are poorly correlated (Johnson and others 1995). Both species are found together in black spruce (*Picea mariana*) forests (Foote 1983), from lowland bogs to upland well-drained sites (Vander Kloet 1988) and alpine tundra. Both are facultative resprouters, resprouting from fire-pruned aerial stems or rhizomes (Viereck and Schandelmeier 1980; Calmes and Zasada 1982).

Sparse data indicate that blueberry and lingonberry produce more abundant berry crops in black spruce forest approximately 3–30 years post-fire than in dense deciduous or coniferous forests. Berry production requires an open canopy, adequate soil moisture, and the presence of a pre-fire *Vaccinium* population from which to resprout. In a Russian wildfire chronosequence, blueberry and *Oxycoccus quadripetalus* (cranberry) began fruit-bearing 3 years post-fire. Blueberry yield was 2.6-fold higher than in the unburned control a year after fruiting began, likely due to increased light availability that persisted for 17 years post-fire (Mironov 1984). Both types of berries were larger than those in unburned plots and more resistant to damage. In interior Alaska, berry fruiting by several species (genera *Vaccinium*, *Viburnum*, *Geocaulon*, *Cornus*, and *Empetrum*) was sufficient 4 years after a severe fire in black spruce for red-backed voles to recolonize and overwinter in the area (West 1982).

Fire severity strongly shapes the timing of positive berry response to fire (Rowe 1983). After a light-to-moderate ground fire, blueberry and lingonberry may return to or exceed pre-fire vegetative biomass in a few years (Uggla 1959); after a more severe fire, recovery may take more than 5–

10 years (Viereck and Dyrness 1979; Schimmel and Granstrom 1996). Severe fires are likely to delay recovery of berry production by burning the organic mat and increasing damage to the below-ground parts of plants (Calmes and Zasada 1982), especially in the more shallowly rooted *V. vitis-idaea* (Uggla 1959; Friedman 1981). Where the organic mat is burned away to mineral soil, belowground stems and seeds of both species are typically killed, and seeds must disperse from outside the burn for recruitment to occur (Viereck and Schandelmeier 1980; Calmes and Zasada 1982).

DISCUSSION

Subsistence species inhabiting boreal forests in interior Alaska and adjacent Canada exhibit distinct changes in post-fire population density and varied preferences for post-fire habitat of different ages (Table 1 and Figure 4). Two highly contrasting species, in terms of foraging needs, are moose and caribou. For example, wildfire is reported to benefit moose—a major component of boreal forest subsistence diets—within 10–30 years. In contrast, fire leads to decreased wintertime use by caribou, another important game species, for several decades or longer. These differences largely reflect contrasting diets, with moose favoring early successional, resprouting shrubs and saplings and caribou requiring late-successional vegetation such as lichens in mature spruce forests. Also, moose populations have a greater potential to respond numerically to fire than do caribou because cow moose can produce twin calves when in good nutritional condition (caribou rarely produce twins). Twinning rate in moose populations is negatively correlated to population density (Boertje and others 2007), but a burn could improve the

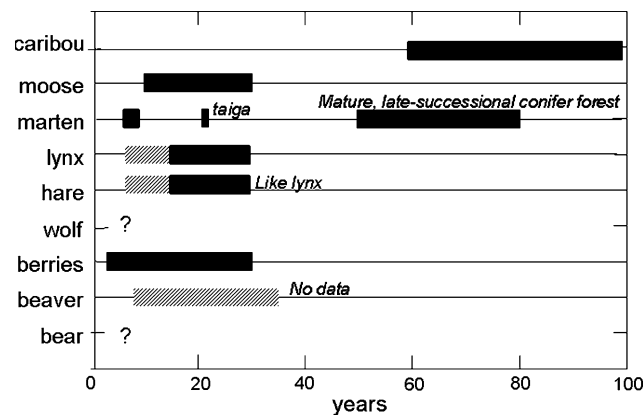


Figure 4. Approximate optimal periods post-fire for density or productivity of key boreal forest subsistence species, according to the ecological literature. Hatched bars indicate uncertain or hypothetical information.

nutritional condition of a herd by enhancing availability and quality of winter forage. Changing fire frequency could therefore have contrasting effects on human communities that differ in their relative harvests of moose versus caribou.

Most studies that we reviewed focused on stand-scale fire effects, through comparisons of use between burned and unburned stands. However, most subsistence species use multiple stands. Moose and snowshoe hares often use burn edges to capture improved forage in the burns and predator protection in adjacent unburned forest. Marten, lynx, and bear appear to use different habitats for foraging, including more open or younger stands, than for hibernation and breeding, when structural features often associated with mature forest are important. Other species, including caribou and most predators, move extensively among stands. Conclusions about fire effects on wildlife based on stand-level studies should therefore be extrapolated to landscape scales with caution. To conclude that a majority of subsistence species use and benefit from 10- to 35-year-old forest—and communities would therefore benefit from vast tracts of young- to intermediate-aged forest—would reflect wildlife foraging studies, but would overlook life-cycle needs for denning, calving, and predator protection (structure of old, fallen trees, edge environments, and sufficient cover). One method for connecting stand-level preferences to landscape responses is with spatially explicit simulation models, the primary tools for exploring alternative future scenarios at the landscape level (Turner 2005). Rupp and others (2006) built a simulation model of caribou winter habitat availability in the Alaskan boreal forest under a range of fire regimes. Analysis revealed marked decreases in spruce-lichen habitat area and in spatial heterogeneity across a range of increases in fire frequency and size.

A review of subsistence species' response to fire is one piece of a complex suite of interactions in a social-ecological study of human–fire interactions in the boreal forest. Our findings suggest that human communities relying on multiple subsistence species are likely to benefit from access to a mosaic of forest patches that vary in time since fire. Two processes are currently altering landscape configuration: (1) Fire suppression is reducing annual area burned close to communities (DeWilde and Chapin 2006; Calef and others in press). If this continues, it will lead to a larger proportion of late-successional black spruce near communities (model prediction from Chapin and others 2003). (2) However, in areas without fire suppression, fires are becoming

larger. Thus, both near and far from communities, it is increasingly likely that large areas of a single vegetation stage will predominate. Both very young (<15 years) and very old (mature black spruce) stands provide relatively few ecosystem services. Current trends are increasingly likely to present communities with these two stand types. The establishment in the mid-20th century of permanent villages in rural Alaska radically changed traditional human mobility patterns; rather than moving among productive forest patches, community members have a fixed location from which to hunt, fish, or gather. Our findings suggest that communities are unlikely to find or gather abundant food resources if surrounded by large tracts of homogeneous black spruce, homogeneous young forest, or a combination of solely the two. Therefore, a sufficient diversity of patches must be available within travel distance. A mosaic of stand ages affects not only availability of subsistence plants and animals to rural communities, but also the organisms' access to and travel among patches as optimal and suboptimal habitats change in space and time (Wolff 1980). However, overall fire effects on subsistence also depend on factors like ease of travel: some subsistence communities report that post-fire conditions hamper travel and access (Chapin and others 2004). Downed trees, upturned roots, or dense regrowth can inhibit access to traplines, cabins, seasonal routes, and hunting sites.

A complicating factor in forecasting fire effects is fire heterogeneity, including topographic variation, variation in fire severity, areal extent of unburned islands, and fire edge indices. Here, we have treated burned patches as uniform in terms of fire effects upon successional trajectory, because we are assessing stand age in time since last fire. Therefore, directional change toward increased individual fire sizes, frequency, and total area burned would indeed lead to larger, more homogeneous forest patches. For example, several studies (incorporating models, historical data, or a combination) report that predicted climatic warming and fire regimes will likely lead to homogenization of the boreal forest landscape with a higher proportion of early successional stands (Clark 1988; Overpeck and others 1990; Thompson and others 1998; Amiro and others 2001; Turner and others 2003). However, current research also indicates sources of variability. One interior Alaskan study showed that variance in burn severity increases with individual fire size (Duffy and others in press). A Canadian study showed that unburned islands are proportional to burn size (Eberhart and Woodard 1987). Johnstone and Kasischke (2005) showed that in a

1994 Alaskan fire in black spruce, variations in depth of burning in the organic layer led to variation in tree recruitment and shrub and herbaceous layer composition, leading to greater landscape heterogeneity. Post-fire range extension of lodgepole pine (*Pinus contorta*) has been documented in the southern Yukon (Johnstone and Chapin 2003), increasing the post-fire species diversity and landscape heterogeneity. Given the clear dependence of subsistence communities on landscape heterogeneity and the uncertainty in future fire-driven changes in habitat heterogeneity, this is clearly a fertile arena for research.

Fire Management Around Subsistence Communities

Dynamics of fire around human communities in the boreal forest reflect local human management and global-to-regional environmental change. The pattern of human influence on the fire regime is an increase in ignitions and a decrease in the area burned, with a footprint around settlements, highways, and major rivers. Human-caused fire ignitions outnumber lightning-caused ignitions most strongly in a 5-km radius around a settlement (Calef and others in press). Beyond 20 km from a settlement, lightning-caused wildfires predominate, and these fires tend to burn an area, on average, eight times larger than human-caused fires. Therefore, area burned by fire is very low close to settlements and increases with distance until it peaks 35–45 km from villages (Calef and others in press). The case of fire suppression around communities was analyzed with the landscape model ALFRESCO, which simulates climate–fire–vegetation interactions in interior Alaska (Rupp and others 2002). When fire probability was reduced by 50% in the model to simulate effects of fire suppression, there was an increase in the area of unburned black spruce (Chapin and others 2003). Alaska's observed rapid climatic change has also caused increased air temperatures and reduced surface moisture (Serreze and others 2000), thawing of permafrost (Osterkamp and Romanovsky 1999), and increased incidence of insect outbreaks (for example, spruce bark beetle, Berg and others 2006), all of which increase fire risk due to drying of fuels. An important function of permafrost is as an impervious surface holding groundwater close to the soil surface (Viereck 1973); as permafrost thaws, the overlying soil is better drained and vegetation may dry. In insect outbreaks, feeding by bark beetles can alter accumulation of fuels through tree mortality and opening of the forest

canopy to solar insolation (McCullough and others 1998). Finally, land use change—such as conversion to agriculture—and logging have altered the southern boreal forest of Alaska.

What are potential management options to support the flows of ecosystem goods and services in a changing environment? Policies that reduce the rate of climate disruption would address an important cause of recent changes. National and state fire policy tools that could address wildlife habitat needs include (a) wildland fire use, which shapes wildfires already burning through cutting of fire lines, fuel removal, and promotion of fire in desired locations; (b) prescribed fires, which are becoming politically and ecologically more difficult to conduct in Alaska; and (c) fuels thinning and management. Fires are allowed to burn and are simply monitored from the air in about two-thirds of Alaska, so the natural experiment of wildfire without suppression is already being conducted (DeWilde and Chapin 2006). Fires have been suppressed for decades in the vicinity of settlements, roads, and some rivers. The modeled result of fire suppression is an increase in the areal extent of late-successional black spruce and white spruce (*Picea mariana* and *P. glauca*), which increases the potential for large future fires (Chapin and others 2003). Public education and stakeholder discussion will continue to be part of management options and decisions. After the Alaskan wildfire season of 2004, the largest on record, public meetings showed a call for more fire suppression around cities and towns (Todd and Jewkes 2006). One example of collaborative fire management comes from the Koyukuk and Nowitna National Wildlife Refuges in interior Alaska. There, one fire management officer has conducted fuels thinning treatments around communities in collaboration with the indigenous Tribal Council in each community. He also orchestrated a prescribed burn program in a slough area where fires in the 1940s and 1970s were suppressed. The planned sequence of burns is intended to prevent unwanted fire effects on vegetation and to benefit marten, weasel, muskrat, moose, and migratory waterfowl and songbirds. Another example involves fire suppression to protect lichen habitat which serves as caribou winter forage: in a collaborative management agreement in 2006 between the Kanuti National Wildlife Refuge, Alaska Fire Service, and the regional Native corporation, Doyon, Inc., the lead Refuge biologist initiated an increase in fire suppression levels from “Limited” to “Modified” suppression (L. Saperstein and M. Spindler, USFWS, pers. comm.).

Further Research Needs

Although some information exists about the effects of fire frequency or time since fire on many key subsistence species in the boreal forest, many research gaps persist. There is a growing body of literature on the effects of fire severity on boreal species and ecosystem processes (for example, Johnstone and Kasischke 2005; Johnstone and Chapin 2006) and effects of fire size or shape on boreal species (Johnstone and Kasischke 2005; Maier and others 2005; Duffy and others in press). Little information exists to support inferences about how fires occurring in different vegetation types or stand ages might vary in their effects on subsistence resources. Almost none of the studies we reviewed address the effects of longer-term fire history or of repeated burns at changing intervals. In particular, very little data exist on large carnivores and aquatic habitats. Species interactions are extremely important for population dynamics and therefore subsistence harvests, but we did not find comprehensive research on species interactions in post-fire environments for the 17 subsistence species reviewed here. Because there are few papers that address fire and subsistence species interactions (see Fisher and Wilkinson 2005; Hood and others 2007; Pastor and others 1988; Schwartz and Franzmann 1989, 1990; and outside the boreal forest, Bailey and Whitham 2002), our review generally covers one species at a time. Finally, existing studies are short in duration and occur at relatively small spatial scales. More long-term, spatially extensive observations will be needed to deduce patterns of response across all of these variables. In this respect, local knowledge and observations could complement and significantly add to the information available from ecological research to assess biodiversity trends linked to climate and fire regime changes and their impact on human well-being (for example, Huntington and others 2004). Such an integrated approach could build the capacity to anticipate and plan for change.

ACKNOWLEDGMENTS

Funding for the research was provided by the Alaska Human–Fire Interaction project (NSF grant OPP-0328282) and the Science, Technology, Engineering, Policy and Society (STEPS) Institute of the University of California, Santa Cruz. We extend our thanks to the following people and organizations for their insights, suggestions, and contributions: Sarah Trainor, David McGuire, Scott Rupp, Paul Duffy, Henry Huntington, Orville Huntington, David Natcher, Monika Calef and Roz Naylor of the

Human–Fire Interactions group; Yair Chaver; Kris Hulvey and Jae Pasari at UCSC; Jenny Bryant, Joe Huhndorff, Robert Lambrecht, Karin Lehmkuhl, Brad Scotton, Mike Spindler, and Lisa Saperstein of USFWS; Tom Paragi of Alaska Dept. of Fish and Game; and Loudon Tribal Council, Galena, Alaska. In addition, we thank Dr. Eric Kasischke and an anonymous reviewer for their comments and suggestions, which greatly improved the manuscript.

REFERENCES

- ACIA. 2005. Arctic Climate Impact Assessment (ACIA). Cambridge: Cambridge University Press.
- Adams L, Eastland W, Jandt R, Haggstrom DA. 2004. Burned area emergency stabilization and rehabilitation plan: 2004 Alaska fires. Wildlife Resource Assessment. US Geological Survey, Bureau of Land Management, Bureau of Indian Affairs, and Alaska Department of Fish and Game, Anchorage, Fairbanks, and Juneau, Alaska. http://www.ak.blm.gov/baer/plan/assessments/final_wildlifeassess.doc.
- Alaska Geospatial Data Center, Wildland Fire Dataset, <http://agdc.usgs.gov/data/blm/fire/index.html>.
- Alt K. 1994. Whitefish species. Wildlife notebook series. Alaska Department of Fish and Game. <http://www.adfg.state.ak.us/pubs/notebook/fish/whitfish.php>.
- Amiro BD, Stocks BJ, Alexander ME, Flannigan MD, Wotton BM. 2001. Fire, climate change, carbon and fuel management in the Canadian boreal forest. *Int J Wildland Fire* 10:405–13.
- Arseneault D, Villeneuve N, Boismenu C, Leblanc Y, Deshayes J. 1997. Estimating lichen biomass and caribou grazing on the wintering grounds of northern Quebec: an application of fire history and Landsat data. *J Appl Ecol* 34:65–78.
- Arthur SM, Krohn WB, Gilbert JR. 1989. Habitat use and diet of fishers. *J Wildlife Manag* 53:680–8.
- Bailey JK, Whitham TG. 2002. Interactions among fire, aspen, and elk affect insect diversity: reversal of a community response. *Ecology* 83:1701–12.
- Ballard WB, Krausman PR, Boe S, Cunningham S, Whitlaw HA. 2000. Short-term response of Gray Wolves, *Canis lupus*, to wildfire in Northwestern Alaska. *Can Field-Nat* 114:241–7.
- Barnes DM, Mallik AU. 2001. Effects of Beaver, *Castor canadensis*, herbivory on streamside vegetation in a northern Ontario watershed. *Can Field-Nat* 115:9–21.
- Berg EE, Henry JD, Fastie CL, De Volder AD, Matsuoka S. 2006. Long-term histories of spruce beetle outbreaks in spruce forests on the western Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationships with summer temperature. *Forest Ecol Manag* 227:219–32.
- Blanchard B, Knight RR. 1990. Reactions of grizzly bears, *Ursus arctos horribilis*, to wildfire in Yellowstone National Park, Wyoming. *Can Field-Nat* 104:592–4.
- Boertje RD, Kellie KA, Seaton CT, Keech MA, Young DD, Dale BW, Adams LG, Aderman AR. 2007. Ranking Alaska moose nutrition: signals to begin liberal antlerless harvests. *J Wildlife Manag* 71:1494–506.
- Bonan GB, Shugart HH. 1989. Environmental factors and ecological processes in boreal forests. *Annu Rev Ecol Syst* 20:1–28.
- Brand CJ, Keith LB, Fischer CA. 1976. Lynx responses to changing snowshoe hare densities in Central Alberta. *J Wildlife Manag* 40:416–28.

- Buskirk SW. 1994. Introduction to the genus *Martes*. In: Buskirk SW, Harestad AS, Raphael MG, Powell RA, Eds. Martens, sables, and fishers: biology and conservation. Ithaca and London: Cornell University Press. pp 1–10.
- Buskirk SW, Powell RA. 1994. Habitat ecology of fishers and American martens. In: Buskirk SW, Harestad AS, Raphael MG, Powell RA, Eds. Martens, sables, and fishers: biology and conservation. Ithaca and London: Cornell University Press. pp 283–96.
- Calef MP, McGuire AD, Chapin FS, III. Human influences on wildfire in Alaska from 1988 to 2005: An analysis of the spatial patterns of human impacts. *Earth Interact* (in press).
- Calmes MA, Zasada JC. 1982. Some reproductive traits of four shrub species in the black spruce forest type of Alaska. *Can Field-Nat* 96:35–40.
- Cederlund GH, Okarma H. 1988. Home range and habitat use of adult female moose. *J Wildlife Manag* 52:336–43.
- Chapin FS III, Rupp TS, Starfield AM, DeWilde LO, Zavaleta ES, Fresco N, Henkelman J, McGuire AD. 2003. Planning for resilience: modeling change in human–fire interactions in the Alaskan boreal forest. *Front Ecol Environ* 1:255–61.
- Chapin, FS, III, Trainor SF, Huntington HP, Natcher DC, Village of Huslia, Alaska. 2004. Huslia tribal gatherings on climate change and fire: January 7–10, March 8–11, and October 4–6, 2004. Summary comments about fire Tribal Council of Huslia, Western Regional Advisory Council, and University of Alaska, Fairbanks, Huslia, Alaska..
- Chapin FS III, Viereck LA, Adams PC, Van Cleve K, Fastie CL, Ott RA, Mann D, Johnstone JF. 2006. Successional processes in the Alaskan boreal forest. In: Chapin FS III, Oswood MW, Cleve KVan, Viereck LA, Verbyla DL, Eds. Alaska's Changing Boreal Forest. Oxford and New York: Oxford University Press. pp 100–20.
- Clark JS. 1988. Effect of climate change on fire regimes in northwestern Minnesota. *Nature* 334:233–5.
- Collins WB, Helm DJ. 1997. Moose, *Alces alces*, habitat relative to riparian succession in the boreal forest, Susitna River, Alaska. *Can Field-Nat* 111:567–74.
- Cowan IM, Mackay RH. 1950. Food habits of the marten, *Martes americana*, in the Rocky Mountain region of Canada. *Can Field-Nat* 64:100–4.
- Delaney K. 1994. Chinook salmon. Wildlife notebook series. Alaska Department of Fish and Game. [http://www.adfg-state.ak.us/pubs/notebook/fish/chinook.php](http://www.adfg.state.ak.us/pubs/notebook/fish/chinook.php).
- DeWilde L, Chapin FS III. 2006. Human impacts on the fire regime of interior Alaska: interactions among fuels, ignition sources, and fire suppression. *Ecosystems* 9:1342–53.
- Duffy PA, Epting J, Graham JM, Rupp TS, McGuire AD. 2007. Analysis of Alaskan burn severity patterns using remotely-sensed data. *Int J Wildland Fire* 16:277–284.
- Eberhart KE, Woodard PM. 1987. Distribution of residual vegetation associated with large fires in Alberta. *Can J Forest Res* 17:1207–12.
- Ellison LN. 1975. Density of Alaskan spruce grouse before and after fire. *J Wildlife Manag* 39:468–71.
- Errington PL. 1963. Muskrat populations. Ames, Iowa: Iowa State University Press.
- Fall JA. 1990. The Division of Subsistence of the Alaska Department of Fish and Game: an overview of its research program and findings: 1980–1990. *Arctic Anthropol* 27:68–92.
- Fisher JT, Wilkinson L. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Rev* 35:51–81.
- Flannigan MD, Logan KA, Amiro BD, Skinner WR, Stocks BJ. 2005. Future area burned in Canada. *Climatic Change* 72:1–16.
- Foote MJ. 1983. Classification, description, and dynamics of plant communities after fire in the taiga of interior Alaska. Research Paper PNW-307 Research Paper PNW-307. Portland, Oregon: US Department of Agriculture, Forest Service Pacific Northwest Research Station..
- Friedman BF. 1981. Fire ecology and population biology of two taiga shrubs, Lingonberry, *Vaccinium vitis-idaea* and Alpine Blueberry, *Vaccinium uliginosum*. MS Thesis. University of Alaska, Fairbanks.
- Gasaway WC, Dubois SD. 1985. Initial response of moose, *Alces alces*, to a wildfire in interior Alaska. *Can Field-Nat* 99:135–40.
- Gasaway WC, Dubois SD, Boertje RD, Reed DJ, Simpson DT. 1989. Response of radio-collared moose to a large burn in central Alaska. *Can J Zool* 67:325–9.
- Grange WB. 1932. Observations on the snowshoe hare, *Lepus americanus phaeonontus* Allen. *J Mammal* 13:1–19.
- Gresswell RE. 1999. Fire and aquatic ecosystems in forested biomes of North America. *Trans Am Fish Soc* 128:193–221.
- Hakala JB, Seemel RK, Richey RA, Kurtz JE. 1971. Fire effects and rehabilitation methods: Swanson–Russian Rivers fires. In: Slaughter CW, Barney RJ, Hansen GM, Eds. Fire in the northern environment. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, University of Alaska College (Fairbanks). pp 87–99.
- Hamer D. 1996. Buffaloberry, *Shepherdia canadensis* (L) Nutt, fruit production in fire-successional bear feeding sites. *J Range Manag* 49:520–9.
- Harris LD. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. Chicago, Illinois: University of Chicago Press.
- Hood GA, Bayley SE, Olson W. 2007. Effects of prescribed fire on habitat of beaver (*Castor canadensis*) in Elk Island National Park, Canada. *Forest Ecol Manag* 239:200–9.
- Howell PJ. 2001. Effects of disturbance and management of forest health on fish and fish habitat in eastern Oregon and Washington. *Northwest Sci* 75:157–65.
- Huntington HP, Callaghan T, Fox S, Krupnik I. 2004. Matching traditional and scientific observations to detect environmental change: a discussion on Arctic terrestrial ecosystems. *Ambio* 33:18–23.
- Huntington HP, Trainor SF, Natcher DC, Huntington OH, DeWilde L, Chapin FS, III. 2006. The significance of context in community-based research: understanding discussions about wildfire in Huslia, Alaska. *Ecol Soc* 11(1):40. [online] URL: <http://www.ecologyandsociety.org/vol11/iss1/art40/>.
- Jandt RR. 1992. Modeling moose density using remotely sensed habitat variables. *Alces* 28:41–57.
- Johnson EA, Rowe JS. 1975. Fire in the subarctic wintering ground of the Beverley Caribou Herd. *Am Midland Nat* 94:1–14.
- Johnson WN, Paragi TF, Katnik DD. 1995. The relationship of wildland fire to lynx and marten populations and habitat in interior Alaska. Final Report U.S. Fish and Wildlife Service, Galena, Alaska.

- Johnstone JF, Chapin FS III. 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biol* 9:1401–9.
- Johnstone JF, Chapin FS III. 2006. Effects of burn severity on patterns of post-fire tree recruitment in boreal forests. *Ecosystems* 9:14–31.
- Johnstone JF, Kasischke ES. 2005. Stand-level effects of soil burn severity on post-fire regeneration in a recently-burned black spruce forest. *Can J Forest Res* 35:2151–63.
- Joly K, Dale BW, Collins WB, Adams LG. 2003. Winter habitat use by female caribou in relation to wildland fires in interior Alaska. *Can J Zool* 81:1192–201.
- Kafka V, Gauthier S, Bergeron Y. 2001. Fire impacts and crowning in the boreal forest: study of a large wildfire in western Quebec. *Int J Wildland Fire* 10:119–27.
- Kasischke ES, Rupp TS, Verbyla DL. 2006. Fire trends in the Alaskan boreal forest. In: Chapin FS III, Yarie J, Cleve KVan, Viereck LA, Oswood MW, Verbyla DL, Eds. *Alaska's Changing Boreal Forest*. New York: Oxford University Press. pp 285–301.
- Kasischke ES, Turetsky M. 2006. Recent changes in the fire regime across the North American boreal region—Spatial and temporal patterns of burning across Canada and Alaska. *Geophys Res Lett.*
- Kasischke ES, Williams D, Barry D. 2002. Analysis of the patterns of large fires in the boreal forest region of Alaska. *Int J Wildland Fire* 11:131–44.
- Keith LB, Surrendi PC. 1971. Effects of fire on a snowshoe hare population. *J Wildlife Manag* 35:16–26.
- Kelsall JP, Telfer ES, Wright TD. 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: Canadian Wildlife Service.
- Klein DR. 1982. Fire, lichens, and caribou. *J Range Manag* 35:390–5.
- Koehler GM. 1990. Population and habitat characteristics of lynx and snowshoe hares in North Central Washington. *Can J Zool* 68:845–51.
- Koehler GM, Hornocker MG. 1977. Fire effects on marten habitat in Selway-Bitterroot Wilderness. *J Wildlife Manag* 41:500–5.
- Krupnik I, Jolly D, Eds. 2002. *The earth is faster now: indigenous observations of arctic environmental change*. Fairbanks, Alaska: Arctic Research Consortium of the United States.
- Latour PB, Maclean N, Poole KG. 1994. Movements of martens, *Martes americana*, in burned and unburned taiga in the Mackenzie Valley, Northwest Territories. *Can Field-Nat* 108:351–4.
- Lehmkuhl KL. 2000. Population dynamics and ecology of yellow-cheeked voles (*Microtus xanthognathus*) in early post-fire seres of interior Alaska. MS Thesis. University of Alaska, Fairbanks.
- Lensink CJ, Skoog RO, Buckley JL. 1955. Food habits of marten in interior Alaska and their significance. *J Wildlife Manag* 19:364–8.
- Leopold AS, Darling FF. 1953. Effects of land use on moose and caribou in Alaska. 18th North American Wildlife Conference. pp 553–62.
- Litvaitis JA, Sherburne JA, Bissonette JA. 1985. Influence of understory characteristics on snowshoe hare habitat use and density. *J Wildlife Manag* 49:866–73.
- Loranger AJ, Bailey TN, Lamed WW. 1991. Effects of forest succession after fire in moose wintering habitats on the Kenai Peninsula, Alaska. *Alces* 27:100–9.
- Lotspeich FB, Mueller EW, Frey PJ. 1970. Effects of large-scale forest fires on water quality in interior Alaska. Fairbanks: US Department of the Interior, Federal Water Pollution Control Administration, Alaska Water Laboratory..
- Lutz HJ. 1956. Ecological effects of forest fires in the interior of Alaska. U.S. Department of Agriculture Tech. Bull. No. 1133..
- MacCracken JG, Viereck LA. 1990. Browse regrowth and use by moose after fire in interior Alaska. *Northwest Sci* 64:11–8.
- Magoun AJ. 1991. *Wildfire and furbearers in the boreal forest with emphasis on marten, lynx, and their prey: an annotated bibliography*. U.S. Fish and Wildlife Service—National Park Service, U.S. Department of the Interior.
- Magoun AJ, Vernam DJ. 1986a. An evaluation of the Bear Creek burn as marten (*Martes americana*) habitat in interior Alaska. Final report, Special cooperative project AK-950-CAH-0. Fairbanks, Alaska: U.S. Bureau of Land Management and Alaska Department of Fish and Game.
- Magoun AJ, Vernam DJ. 1986b. An evaluation of the Bear Creek burn as marten (*Martes americana*) habitat in interior Alaska. Final report, Special cooperative project AK-950-CAH-0. Fairbanks, Alaska: U.S. Bureau of Land Management and Alaska Department of Fish and Game.
- Maier JAK, Ver Hoef JM, McGuire AD, Bowyer RT, Saperstein L, Maier HA. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. *Can J Forest Res* 35:2233–43.
- Martin SK. 1994. Feeding ecology of American martens and fishers. In: Buskirk SW, Harestad AS, Raphael MG, Powell RA, Eds. *Martens, sables, and fishers: biology and conservation*. Ithaca, New York: Cornell University Press. pp 297–315.
- McCullough DG, Werner RA, Neumann D. 1998. Fire and insects in northern and boreal forest ecosystems of North America. *Annu Rev Entomol* 43:107–27.
- McCullough DG, Spalding S, Sturdevant D, Hicks M. 2001. Summary of technical literature examining the physiological effects of temperature on salmonids. U.S. Environmental Protection Agency Report EPA-910-D-01-005, Seattle.
- Miller DR. 1980. Wildfire effects on barren-ground caribou wintering on the taiga of north-central Canada. In: Reimers E, Gaare E, Skjemneberg S, Eds. *The second annual international reindeer/caribou symposium*. Trondheim, Norway: Direktoratet for vilt og ferskvannsfisk. pp 84–9.
- Minshall GW, Brock JT, Varley JD. 1989. Wildfires and Yellowstone's stream ecosystems. *Bioscience* 39:707–15.
- Mironov KA. 1984. Recovery of bog bilberry and cranberry after ground fires. *Sov J Ecol* 14:199–204.
- Mowat G, Slough B. 2003. Habitat preference of Canada lynx through a cycle in snowshoe hare abundance. *Can J Zool* 81:1736–45.
- Murphy PJ, Mudd JP, Stocks BJ, Kasischke ES, Barry D, Alexander ME, French NHF. 2000. Historical fire records in the North American boreal forest. In: Kasischke ES, Stocks BJ, Eds. *Fire, climate change and carbon cycling in the North American boreal forests*. New York: Springer-Verlag. pp 274–88.
- Natcher DC. 2004. Implications of fire policy on Native land use in the Yukon Flats, Alaska. *Human Ecol* 32:421–41.
- Nellis CH, Wetmore SP, Keith LB. 1972. Lynx–prey interactions in central Alberta. *J Wildlife Manag* 36:320–8.

- O'Donoghue M, Boutin S, Krebs CJ, Murray DL, Hofer EJ. 1998. Behavioral responses of coyotes and lynx to the snowshoe hare cycle. *Oikos* 82:169–83.
- Osterkamp TE, Romanovsky VE. 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost Periglacial Processes* 10:17–37.
- Overpeck JT, Rind D, Goldberg R. 1990. Climate-induced changes in forest disturbance and vegetation. *Nature* 343:51–3.
- Paragi TF, Johnson WN, Katnik DD, Magoun AJ. 1996. Marten selection of postfire seres in the Alaskan taiga. *Can J Zool* 74:2226–37.
- Paragi TF, Johnson WN, Katnik DD, Magoun AJ. 1997. Selection of post-fire seres by lynx and snowshoe hares in the Alaskan taiga. *Northwestern Nat* 78:77–86.
- Pastor J, Naiman RJ, Dewey B, McInnes P. 1988. Moose, microbes, and the boreal forest. *Bioscience* 38:770–7.
- Peek JM. 1974. Initial response of moose to a forest fire in northeastern Minnesota. *Am Midland Nat* 91:435–8.
- Peterson RO, Wollington JD, Bailey TN. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monogr* 88:1–52.
- Pickett STA, White PS, Eds. 1985. The ecology of natural disturbance and patch dynamics. New York: Academic Press.
- Pietz PJ, Tester JR. 1983. Habitat selection by snowshoe hares in north central Minnesota. *J Wildlife Manag* 47:686–96.
- Rieman B, Clayton J. 1997. Wildfire and native fish: issues of forest health and conservation of sensitive species. *Fisheries* 22:6–15.
- Romme WH, Knight DH. 1982. Landscape diversity: the concept applied to Yellowstone Park. *Bioscience* 32:664–70.
- Rowe JS. 1983. Concepts of fire effects on plant individuals and species. In: Wein RW, MacLean DA, Eds. The role of fire in northern circumpolar ecosystems. New York: John Wiley and Sons, Ltd. pp 135–54.
- Rupp TS, Olson M, Adams LG, Dale BW, Joly K, Henkelman J, Collins WB, Starfield AM. 2006. Simulating the influences of various fire regimes on caribou winter habitat. *Ecol Appl* 16:1730–43.
- Rupp TS, Starfield AM, Chapin FS, Duffy P. 2002. Modeling the impact of black spruce on the fire regime of Alaskan boreal forest. *Climatic Change* 55:213–33.
- Saperstein L, Joly K. 2001. The role of wildland fire in caribou ecology: an annotated bibliography. US Geological Survey Alaska Science Center. <http://www.absc.usgs.gov/research/caribou/AnnBib-04-04-01.pdf>.
- Schaefer JA, Pruitt WO. 1991. Fire and woodland caribou in southeastern Manitoba. *Wildlife Monogr* 116:1–39.
- Schimmel J, Granstrom A. 1996. Fire severity and vegetation response in the boreal Swedish forest. *Ecology* 77:1436–50.
- Schwartz CC, Franzmann AW. 1989. Bears, wolves, moose and forest succession; some management considerations on the Kenai Peninsula. *Alces* 25:1–10.
- Schwartz CC, Franzmann AW. 1990. Interrelationship of black bears to moose and forest succession in the Northern coniferous forest. *Wildlife Monogr* 113:1–58.
- Scott C, Brown LA, Jennings GB, Utermohle CJ. 2001. Community Profile Database for Access 2000 (version 3.12). Juneau: Alaska Department of Fish and Game, Division of Subsistence.
- Scotter GW. 1971a. Fire, vegetation, soil, and barren-ground caribou relations in northern Canada. Fire in the Northern Environment, Fairbanks, Alaska. pp 209–30.
- Scotter GW. 1971b. Wildfires in relation to the habitat of the barren-ground caribou in the taiga of northern Canada. Proceedings of the 10th tall timbers fire ecology conference. pp 85–105.
- Serreze MC, Walsh JE, Chapin FSI, Osterkamp T, Dyurgerov M, Romanovsky VE, Oechel WC, Morison J, Zhang T, Barry RG. 2000. Observational evidence of a recent change in the northern high-latitude environment. *Climatic Change* 46:159–207.
- Sharp WM. 1971. The role of fire in ruffed grouse habitat management. Proceedings of the 10th tall timbers fire ecology conference. pp 47–61.
- Skooog RO. 1968. Ecology of the caribou (*Rangifer tarandus granti*) in Alaska. PhD Dissertation. University of California, Berkeley.
- Skuncke F. 1969. Reindeer ecology and management in Sweden. Biol Paper No 8, University of Alaska, as cited in Viereck and Schandelmeier 1980.
- Slough BG. 1999. Characteristics of Canada Lynx, *Lynx canadensis*, maternal dens and denning habitat. *Can Field-Nat* 113:605–8.
- Slough BG, Sadleir RMFS. 1977. A land capability classification for beaver (*Castor canadensis* Kuhl). *Can J Zool* 55:1324–35.
- Spencer DL, Hakala J. 1964. Moose and fire on the Kenai. Proceedings of the 3rd tall timbers fire ecology conference. pp 10–33.
- Stephenson RO. 1984. The relationship of fire history to fur-bearer populations and harvest. Final Report, W-22-2, Job 7.13R, Juneau: Alaska Department of Fish and Game.
- Stocks BJ, Fosberg MA, Wotton MB, Lynham TJ, Ryan KC. 2000. Climate change and forest fire activity in North American boreal forests. In: Kasischke ES, Stocks BJ, Eds. Fire, Climate Change, and Carbon Cycling in the Boreal Forest. New York: Springer-Verlag. pp 368–76.
- Thomas DC, Barry SJ, Alaie G. 1996. Fire-caribou-winter range relationships in northern Canada. *Rangifer* 16:57–67.
- Thompson ID, Flannigan MD, Wotton BM, Suffling R. 1998. The effects of climate change on landscape diversity: an example in Ontario forests. *Environ Monit Assess* 49:213–33.
- Tietje WM, Ruff RL. 1980. Denning behavior of black bears in boreal forest of Alberta. *J Wildlife Manag* 44:858–70.
- Todd SK, Jewkes HA. 2006. Wildland fire in Alaska: a history of organized fire suppression and management in the last frontier. Bulletin No. 114. Fairbanks, Alaska: University of Alaska Agricultural and Forestry Experiment Station.
- Tonn WM, Boss SM, Aku PK, Scrimgeour GJ, Paszkowski CA. 2004. Fish assemblages in subarctic lakes: does fire affect fish-environment relations in Northern Alberta? *Trans Am Fish Soc* 133:132–43.
- Tonn WM, Paszkowski CA, Scrimgeour GJ, Aku PKM, Lange M, Prepas EE, Westcott K. 2003. Effects of forest harvesting and fire on fish assemblages in Boreal Plains lakes: a reference condition approach. *Trans Am Fish Soc* 132:514–23.
- Turner MG. 1989. Landscape ecology: the effect of pattern on process. *Annu Rev Ecol Syst* 20:171–97.
- Turner MG. 2005. Landscape ecology: what is the state of the science?. *Annu Rev Ecol Syst* 36:319–44.
- Turner MG, Collins SL, Lugo AE, Magnuson JJ, Rupp TS, Swanson FJ. 2003. Disturbance dynamics and ecological response: the contribution of long-term ecological research. *Bioscience* 53:46–56.

- Ugglå E. 1959. Ecological effects of fire on north Swedish forests. Uppsala, Sweden: Institute of Plant Ecology, University of Uppsala, Almqvist and Wiksells Boktryckeri AB.
- Vander Kloet SP. 1988. The genus *Vaccinium* in North America. Ottawa, Canada: Research Branch, Agriculture Canada.
- Viereck LA. 1970. Forest succession and soil development adjacent to the Chena River in interior Alaska. *Arctic Alpine Res* 2:1–26.
- Viereck LA. 1973. Wildfire in the taiga of Alaska. *Quaternary Res* 3:465–95.
- Viereck LA, Dyrness CT. 1979. Ecological effects of the Wickersham Dome fire near Fairbanks, Alaska. General technical report PNW-90. Portland, OR: Pacific Northwest Forest and Range Experiment Station, US Department of Agriculture Forest Service.
- Viereck LA, Schandelmeier LA. 1980. Effects of fire in Alaska and adjacent Canada—a literature review. Alaska Technical Report 6, Anchorage, Alaska: Bureau of Land Management.
- Viereck LA, Van Cleve K, Dyrness CT. 1986. Forest ecosystem distribution in the taiga environment. In: Cleve KVan, Chapin FS, Flanagan PW, Viereck LA, Dyrness CT, Eds. Forest ecosystems in the Alaskan taiga. New York: Springer-Verlag.
- Ward P. 1968. Fire in relation to waterfowl habitat of the delta marshes. Proceedings of the 8th tall timbers fire ecology conference. pp 255–67.
- Weeden RB. 1965. Grouse and ptarmigan in Alaska. Fed Aid Wildl Rest Proj Rept Vol V, Proj W-6-R, Work Plan I. Juneau, Alaska: Alaska Department of Fish and Game.
- Weixelman DA, Bowyer RT, Van Ballenberghe V. 1998. Diet selection by Alaska moose: effects of fire and forest succession. *Alces* 34:213–38.
- West SD. 1982. Dynamics of colonization and abundance in central Alaskan populations of the northern red-backed vole, *Clethrionomys rutilus*. *J Mammal* 63:128–43.
- Wolff JO. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. *Ecol Monogr* 50:111–30.
- Yarie J. 1981. Forest fire cycles and life tables: a case study from interior Alaska. *Can J Forest Res* 11:554–62.