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2

History and Ecology of the Boreal Zone in Ontario

Bruce Winterhalder

2.1. Introduction

This chapter analyzes the climate, landscape, flora, and fauna of the boreal forest in northern Ontario. It emphasizes facets of this ecosystem known to be of importance to humans. Its goal is to establish the context—the mix of physical and biotic factors, some patterned and some irregular in occurrence—in which human adaptation occurs. The boreal forest on first acquaintance can be deceptive. To the passing outsider it is nearly flat, without the vistas that give a landscape an immediate character. Its streams are mostly sluggish, its vegetation diminutive. It feigns monotony over space and time. Yet ecologically it is a habitat vibrant with activity. Although without strong relief, the landscape is strongly differentiated. The populations of plants and animals of the forest interact in a highly dynamic fashion. This chapter describes the forest in ways that illuminate that differentiation and activity, and attempts to capture its meaning as the context of the adaptation studies which make up the remainder of this volume (see also Kryuchkov, 1976; Pruitt, 1978; Winterhalder, 1977).

The area covered is delimited roughly by the Severn River drainage. At the biome level, it is a study within the Boreal Forest Formation (Rowe, 1972). This ecological zone spans Canada from Newfoundland to the Yukon; it also covers the northern regions of Europe and Asia, often under the name *taiga*. Three subdivisions of the Boreal Forest Formation occur in parts of the Severn drainage. In the southern and central portions is the Northern Coniferous Section, an area of closed black spruce forest interspersed with muskeg and bogs, and stands of jack pine and white birch. The northern one-third of the drainage is the Hudson Bay Lowland Section, an area of open spruce woodlands with extensive muskeg

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and bogs. Occupying a thin strip along the coast of Hudson Bay is the Forest Tundra Section, an area of tundra barrens and isolated clumps of stunted spruce. The Northern Coniferous Section receives the greatest attention in this analysis; Hurlich (1976) provides a more comprehensive description of the Hudson Bay Lowland and Forest Tundra Sections.

The chapter begins with Holocene patterns: glacial retreat and surface geology, climate history, and vegetational and faunal histories. The major part of the chapter is devoted to the contemporary environment. Climate, climatic elements (temperature, precipitation, and wind), and secondary climatic factors (freeze-up and break-up, stream flow, and snow cover) are covered first. Next comes flora, with specific attention to vegetation habitats and the dynamic processes governing their distribution and turnover. A faunal analysis follows, and focuses on moose and snowshoe hare. Sketches for these species show how patterns of population density and dispersion and population responses to environmental factors interact in the boreal forest. On this basis summary information is presented for additional species. The faunal analysis concludes with a brief examination of energy availability and the ecological importance of snow cover. The concluding discussion highlights conceptual lessons of the analysis, with particular attention to the shortcomings of normative description.

2.2. Postglacial History of the Forest

2.2.1. Geology and the Glacial Retreat

The Severn River flows north over the Precambrian Shield and the Hudson Bay Lowlands. The first of these geological regions is a peneplain surface of low relief, the second a contiguous geological basin filled with shallow deposits of shales, limestones, and dolomites (Hewitt and Freeman, 1972: 72–85). Topographic features are shallow. In the Severn area true monadnocks are limited to heights of about 50 m (Moir, 1958: 8).

Glacial influence on the physiography of this region was intense. The late Wisconsin maximum of the Laurentide ice sheet is dated between 19,000 and 16,000 years BP; deglaciation, initiated about 14,000 years BP (Hare, 1976: 509), was well underway by 12,000 years BP (Bird, 1973: 165; see also Dawson, Chapter 3, this volume). By 10,500 years BP the ice margin coincided with the southern edge of the Canadian Shield, and some time before 8000 years BP large pro-glacial lakes developed. Lake Agassiz covered parts of Saskatchewan, Manitoba, Ontario, North Dakota, and Minnesota; Barrow-Ojibway covered much of lower Ontario and Quebec (MacKay, 1963: 17). Immediately following the Cockburn Glacial Phase, a minor readvance about 8500 years BP, the ice sheet disintegrated rapidly in the Hudson Bay region. Saltwater incursion formed the Tyrrell Sea (Bryson *et al.*, 1969: 8), and by 6000–5000 years BP the residual ice masses in Keewatin and Labrador had probably disappeared.

With the opening of a channel toward the northeast, Lake Agassiz drained through the Nelson River into the Tyrrell Sea by 7000 years BP (Elson, 1965). Barrow-Ojibway drained, probably northward, sometime before 7600 years BP (Terasmae, 1970). Due to downwarping of the earth's crust caused by the thick ice sheets, the Tyrrell Sea covered about 70% more area than the present-day Hudson Bay (Andrews, 1973: Fig. 8), which continues to shrink. Isostatic recovery of the land surface under the Bay has totalled 150 m over 6000 years (Andrews, 1973: 189), but historical records from the port of Churchill indicate a reduced contemporary rate of 0.75 m per century (Robinson, 1968: 208). This rapid rebound has lessened the slope into the Bay, and contributed to the poor drainage of northern Ontario (Terasmae, 1961, 1970). The slope presently averages only 0.66 m/km, and where the Hudson Bay Lowland meets the Bay itself the gradient is so slight that, in flying over it, one can hardly define the boundary between the muddy sea and the half-drowned land (Savile, 1968: 398).

The glacial retreat and pro-glacial lakes created the superficial landforms of much of Canada (Prest, 1965: 6–21) and especially those of northern Ontario (Rowe, 1972: 43). Old shorelines of Lake Agassiz are only roughly known in the north, but the western part of the Severn basin was modified by the extinct lake, while that to the east is more directly glacial in origin (Moir, 1958: 11–46). In the west, depressions in the Precambrian peneplain were smoothed by deposits of varved clays laid down in Agassiz or smaller lakes. Surface forms in the east are more commonly irregular deposits of rock till. Moraines, kames, drumlins, and eskers separate kettle lakes in poorly drained depressions. Uplands represent drift deposits, or exposed granites and gneisses.

In the northern parts of the Severn drainage the nearly flat relief of the Hudson Bay Lowland is marked only by shallow, parallel ridges (strand lines). These represent beachlines of the contracting Tyrrell Sea, later Hudson Bay. The surface of the lowland is formed of silts and clays that were deposited in the Tyrrell Sea by rivers draining from the south and west (Robinson, 1968: 215).

Papadakis (1969) identifies the Shield of Northern Ontario as an area of continental podsol soil types. The principal soils are: lithosols, peaty soils, gleisolic soils, podsols, and grey-wooded soils. Each of these soils is associated with specific landform features. Rocky uplands, unfavorable for either soil or vegetation development, are lithosols. Upland areas with coarse drift and good drainage, those supporting forest cover, will generally be podsols or the related but less heavily weathered grey-wooded soils (Rowe, 1972; Tedrow, 1970: 203). Low-lying areas and those with impeded drainage are predominantly gleisolic, or organic or peaty soils (Terasmae, 1970; Moir, 1958: 17).

2.2.2. Climate History

Variations of postglacial climate between 11,000 years BP and the present are fairly well known for the Canadian north from studies of geomorphology,

soil development, vegetation macrofossils, palynology, peat stratigraphy, climatology, and other methods (Andrews, 1973; Davis, 1969; Terasmae, 1973, 1975, 1977; Terasmae and Weeks, 1979; Nichols, 1967, 1969).

Winter weather to the south of the Laurentide ice sheet was probably slightly warmer and summers somewhat cooler than at present. The great depth of the continental ice sheets—2–4 km (Hare, 1976: 508)—would have prevented cold, lower level arctic air from consistently reaching the south (Terasmae, 1973). The climatic amelioration that initiated the Holocene probably occurred rather abruptly, about 11,000 years BP (Ogden, 1967; Webb and Bryson, 1972). Although this change produced a sharp increase in the withdrawal of the ice margin, the physical limitations of melting such a large mass of ice prolonged the contraction for 4000–5000 years (Terasmae, 1973). At its greatest, the rate of retreat was probably around 200–300 m/year (Andrews, 1973).

The postglacial warming reached a maximum at about 7000–5000 years BP (the Hypsithermal Interval). This was a period warmer than the present one, at first drier but then turning moister (Terasmae, 1970). The Hypsithermal was followed by a period of cooling—the Neoglacial (Wright, 1976: 592)—and lesser climatic fluctuations that have continued to the present (Terasmae, 1973: Fig. 9). This description is confirmed by studies in the central subarctic (Nichols, 1967), Manitoba boreal forest (Nichols, 1969), and in central Minnesota (Wright, 1976). It is not clear if the timing and amplitude of this pattern hold over larger areas, nor how far it is possible to refine it into shorter intervals of discrete climates (Wright, 1976). Despite these difficulties, Bradstreet and Davis (1975: 19) reviewed climatic change evidence for eastern Canada and the northeastern United States, and found a consistent picture:

A Hypsithermal period appears to have begun 8500 to 7500 BP and ended 4000 to 3300 BP. The most frequently cited thermal maximum occurred at 5000 BP, with fewer indications for 4000 to 3500 BP. Relatively cool portions of the Hypsithermal may have occurred at about 7000 and 4700 BP, and late-post-glacial cooling since 3300 BP has been interrupted by a warming centered about 2000 to 1500 BP.

This summary parallels Nichol's (1972; cited in Bradstreet and Davis, 1975: 19) and Terasmae's (1973: Fig. 9) interpretations.

More recently, the northern hemisphere experienced a pronounced (by climatological standards) warming trend, beginning about 1885 (Hare and Thomas, 1979). This trend peaked and reversed itself in the 1940s. By 1970 cooling had amounted to half of the post-1885 temperature gain. This trend occurred generally across Canada, but with larger ranges of variability in northern regions (Hare and Thomas, 1979). Although the change of mean annual temperatures through this period is only 0.8°C, it is climatically large and is implicated in faunal redistributions (see Section 2.2.4).

2.2.3. Vegetation History

The Laurentide ice sheet pushed zonal weather and vegetation patterns southward into the northern and central United States, in some instances without

disturbing qualitative relationships within plant communities, and between those communities and climate (Bryson and Wendland, 1967; Terasmae, 1973). Based on palynological reconstruction, late Wisconsin floral assemblages in New England were similar to present-day tundra (distant from trees), while assemblages in the Great Lakes region resembled tundra like that found today near the forest-tundra boundary (Terasmae, 1973; cf. Davis, 1969). "[O]nly a narrow and possibly discontinuous tundra zone [existed] south of the ice margin" (Hare, 1976: 512). But south of this was a broad expanse of forest similar to the contemporary boreal forest.

The flora of northern Canada provides evidence of nearly continuous development and change throughout the Holocene. With glacial retreat, plants migrated northward at rates determined by the colonizing abilities of the species involved, the presence of glacial lakes, and the vast regions of raw soils (Terasmae, 1973; 1977: 10–12). The climate amelioration led by decades or centuries the emergence of soil in particular areas, making it likely that plant communities followed the ice rather closely (Bryson *et al.*, 1969) even though they lagged behind the thermal recovery (Hare, 1976: 515–16). Newly opened areas would have contained a variety of microhabitats, "as a result of soil instability and fluctuating levels of soil moisture—that could accommodate a diverse flora" (Cushing, 1965; quoted in Fitting *et al.*, 1966: 121). Southern Ontario was colonized by tundra and taiga vegetation in the late Wisconsin, and by boreal vegetation in the early Holocene. Somewhat later northern Ontario was colonized by a mix of arctic and boreal species. The more rapid glacial withdrawal in this region, along with favorable climate, lessened the arctic-subarctic zonation when this area was vegetated (Terasmae, 1973; Hare, 1976: 513–15).

Based on dissimilarities between the faunas on the west and east sides of Hudson Bay, MacPherson (1968: 471) believes that a forest cover followed closely the retreat of the ice margin in Ontario. Had a broad tundra zone moved across Ontario south of James and Hudson Bays, population mixing would probably have produced greater faunal congruence between these regions. Hare (1976: 514) has reached the same conclusion using palynological and climatic evidence.

The distribution of tree species in Ontario currently parallels a north-south gradient of climatic adversity. Seventy-five species are endemic in the south; 12 can be found along the shores of James Bay (Rowe, 1966: 18). But it is not only climate that affects this distribution. Extant communities are not in equilibrium. The physiographic surface of northern Ontario is young, and current vegetation patterns reflect the differing capacities of species to migrate, compete, and adapt.

Vegetation—the observable areal aggregations of plants—contains an element of chance, and expresses in its more or less haphazard groupings the continuing, dynamic evolution and migration of plants . . . the distributions of plants and plant aggregations depend not only on climate, but also . . . on history and on physiography, on the age of the land and the nature of its surface, on opportunities for migration, on competition and disturbances. (Rowe, 1966: 22–23)

Long life spans guarantee the slow adjustment of these communities; since colonization only about 100 tree generations have passed in the boreal forest (Boughey, 1962: 73).

Thus, although boreal forest species in some instances quickly reestablished themselves in the north, the vegetation habitat was not necessarily similar to that found today (Hare, 1976). As an example, Terasmae (1973, 1977: 25–26) has noted that muskeg, currently the dominant feature of the northern Ontario landscape, was not common in early postglacial times. The muskeg blanket that covers this region began to develop 6500–5000 years BP, several thousand years after the area was free of ice and pro-glacial lakes. Muskeg species colonize rapidly, little affected by geological or soil substrates. Because of this Terasmae attributes the delay to hydrographic and climatic causes. Muskeg is a “climate-controlled” ecosystem (Terasmae, 1977: 13–18). It became established and flourished in northern Ontario with the wetter and cooler climates that followed the Hypsithermal. Deterioration of the drainage around the margin of Hudson Bay due to isostatic uplift, augmented perhaps by the dams of the ever-industrious beaver (Chapman and Thomas, 1968), probably contributed to this spread of muskeg. Robinson (1968: 217) points out that much of the extensive muskeg mat between the Severn and Albany Rivers was earlier an area of scattered lakes. These are now being filled with sediments and organic materials.

Northern vegetational history is characterized by change and adjustment. In particular, the boreal forest

has no continuity in time, and cannot be thought of as the result of strongly-bound adaptations and adjustments of particular species to one another. It must be explained as a recent adjustment, in a particular environment, rather than the product of community evolution during a long and continuous history. (Davis, 1969: 330)

2.2.4. Faunal History

Little is known about the postglacial fauna of northern Ontario, but the biogeographic histories of animal species in the region have probably been as dynamic as those of plants, and for similar reasons—differing abilities to migrate and compete. These factors plus population tolerances with respect to climate variation and vegetational changes most likely led to a recurrent flux of species, populations, and distributional boundaries throughout this region.

Considerable changes in the ranges of some species have been recorded historically (Urquhart, 1957). Many of these are expansions northward, or east or west above the Great Lakes (a variation on the northward pattern). “It therefore seems logical to assume that all range expansions of native species can be associated with postglacial development” (Peterson, 1957: 43). The best, but not conclusive, evidence for this comes from small mammals (voles and shrews). But some larger mammals, such as moose, appear to follow a similar northward pattern.

There are reasons to doubt, however, that changing distributions of large mammals represent continuation of a post-Pleistocene adjustment. Moose can be cited as an example. Peterson (1957: 46) assembled information showing that their range expanded into northern Ontario following 1875, reaching Hudson Bay in the 1950s. This was interpreted as a postglacial occupation. More recent reports indicate that moose were broadly distributed in the conifer forests of northern Canada prior to the 19th century (Cumming, 1972: 6; Krefting, 1974: 84). Citing Hudson’s Bay Company records from Osnaburgh, Bishop (1974) concurs: “Moose, which had been exterminated from Northern Ontario during the 1820s re-entered the region during the 1890s or early 1900s” (see also Kelsall and Telfer, 1974: 120).

Moose are probably not recent or adventitious animals in the boreal ecosystem. They are a normal component of northern conifer forests, with population densities subject to the vagaries of climate and habitat [summary in Winterhalder (1977: 172–88)] and to human influences (Bishop, 1974; Krefting, 1974; Kelsall and Telfer, 1974). Although Bishop (1974: 91) cites extermination as the reason for the 19th century decline of moose populations in Ontario, decreasing habitat quality or several severe winters could have been the sole or a contributory cause (see Section 2.3.7.1). The climatic amelioration in northern Ontario, beginning in about 1890, or habitat changes resulting from clearing or fires, could account for the recent growth of moose populations there (Kelsall and Telfer, 1974: 117, 126). Both LeResche (1974: 408) and Brassard *et al.* (1974: 68) have expressed the belief that historical population changes interpreted as range expansions are better seen, in some cases, as the result of indigenous population growth. Thus, it may also be the case that moose, while quite scarce, were not entirely absent from the region (Rogers, personal communication; *cf.* Smith, 1975: 22).

Relatively large fluctuations of climate and habitat have occurred in post-glacial northern Ontario. Contemporary observations indicate that similar changes, of smaller amplitude and shorter duration, do have significant biogeographic effects on animal populations. For these reasons historical expansions and contractions of range should probably be taken as indicative of dislocations that would have occurred repeatedly during the Holocene, and have affected many species besides moose.

2.3. Contemporary Environment

2.3.1. Climate

The regions south and west of Hudson Bay are colder than latitude itself would dictate. As troposphere-level winds, the jet streams pass north of the Rockies, curve south around the lower end of Hudson Bay, and then pass north over the Davis Strait, they intensify the cold, high-pressure air masses (anti-

cyclones) lying over the arctic and draw them southeast over central eastern Canada (Thompson, 1968: 265–67). Over the Davis Strait these jet streams influence a low-pressure air mass (cyclone) that is semipersistent in this region (Hare and Thomas, 1979). Counterclockwise circulation of this cyclone, the Icelandic Low, augments the jet streams in drawing cold air to the southeast over the center of the continent. At its source this arctic air is rapidly replenished. The strong net radiation loss associated with the snow cover and polar night of the far north quickly turns invading air masses into cold anticyclones (Bryson and Hare, 1974: 13). The nearly continuous influence of this southeastward flow of cold air has led Hare and Thomas (1979) to call it a “winter monsoon.”

Increasing insolation during spring and summer shifts the jet streams northward, and with them the dominance of arctic air. The Icelandic Low weakens, and warmer air masses from the west and southwest are increasingly important in northern Ontario.

Bryson (1966) has identified the major air masses in central Canada and related them to their sources (Fig. 1). In July northern Ontario is affected by air of mainly arctic and Pacific origin. The modal position of the Arctic Frontal Zone between these air masses lies along the northern edge of the boreal forest. The forest corresponds to the zone of most frequent contact between the mild and generally dry Pacific air (Bryson and Hare, 1974: 4; Hare and Hay, 1974: 52) and the moist arctic air moving off the thawing ice surfaces and cold waters of Hudson Bay and the subarctic to the north (Bryson and Hare, 1974: 29; Savile, 1968). The Arctic Front remains in this northern position well into October, but during November shifts to the southern margin of the boreal forest, where it persists until March (Hare and Hay, 1974: 71). The blustery weather and peak snowfall of November are associated with this transition.

In April and May the Arctic Front breaks up, and arctic air flows in a broad stream, reaching into the central United States. In the north this is a period of cold but relatively stable and fine weather (Bryson, 1966: 253). In June the Arctic Front is reestablished over northern Ontario, completing the annual cycle.

2.3.2. Climatic Elements

2.3.2.1. Temperature

Seasonal temperature changes, represented as maximum and minimum monthly means, are shown in Fig. 2. Unless specified, this and other climatic data are from Big Trout Lake, a community on the northern edge of the Shield and central to both the Severn River drainage and the adaptive studies reported in this volume. The pronounced seasonal cycle is characteristic of continental climates. Minimum daily temperatures rise from a monthly mean of -29°C in January to 11°C in July; maximum daily temperatures rise from a low of -19°C in January to 21°C in July (Fig. 2A). These changes follow closely shifts in the seasonal radiation balance (radiation energy reaching the earth's surface from space, less that which

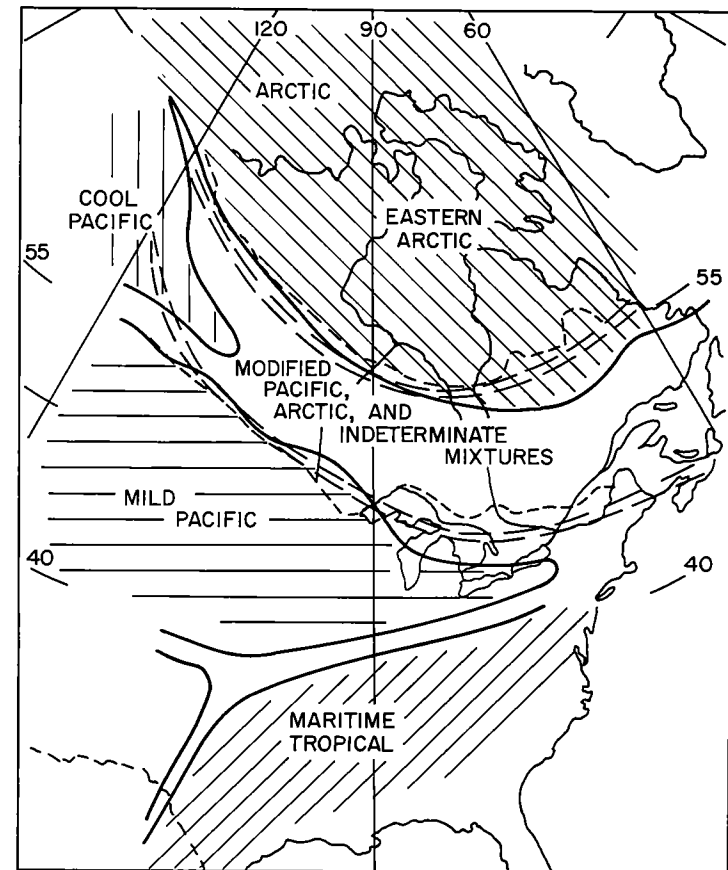


FIGURE 1. Air masses affecting northern Ontario. The hatched areas are affected by the named air masses more than 50% of the time. The modal positions, north and south, respectively, of the summer and winter arctic fronts are shown by the parallel long-dashed lines. The short-dashed lines represent the north and south borders of the boreal forest. After Bryson (1966: 249, Fig. 19, and 266, Fig. 33). Reproduced by permission of the Minister of Supply and Services Canada.

is lost to space), which is positive for this area from March to November (Hare and Thomas, 1979).

Minimum temperature changes lag behind the trend in maximum temperatures throughout the year. In spring increasing insolation warms daytime air temperatures, but lingering ice and snow cover and clear nights (especially in April and May) keep nighttime temperatures low. The converse effect is evident in the fall. Decreased insolation results in lower daytime temperatures, but the large proportion of surface covered with open lakes, and frequent overcast, moderate the nighttime minima. Diurnal temperature ranges are greatest in March, least in October and November.

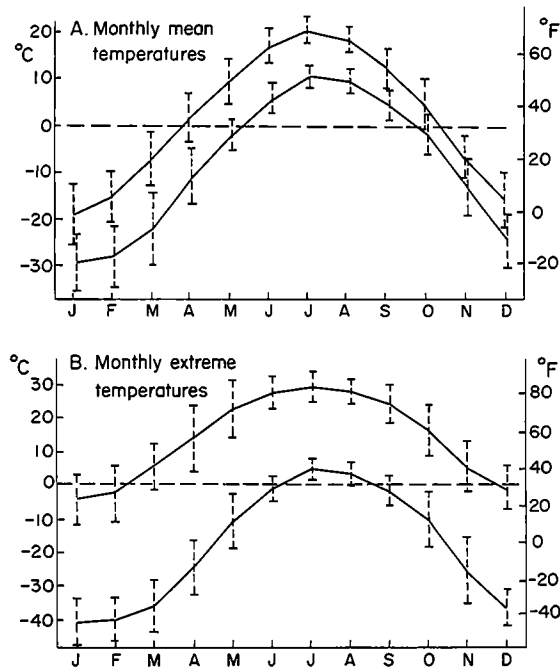


FIGURE 2. Mean and extreme monthly temperatures. (A) Maximum and minimum monthly mean temperatures. (B) Monthly extreme temperatures. The vertical dashed lines indicate the range of variation of the monthly values, ± 2 SD. Data from Big Trout Lake for the period 1939–1967 ($n = 29$) courtesy of the Atmospheric and Environment Service, Dufferin, Ontario.

The range of variability in monthly mean temperatures, shown by the vertical bars in Fig. 2A, grows larger as temperatures decrease. Minimum mean monthly temperatures in March, for instance, can vary over a range of 15°C; in July the corresponding figure is closer to 4°C.

Nearly the same pattern of seasonal changes emerges from Fig. 2B, which summarizes extreme maximum and minimum temperatures. Extreme maxima by month can vary from a low of -12°C in January to 34°C in July. Extreme minima range from -47°C to 8°C . Significantly, thawing daytime (maximum) temperatures can occur in any month, and freezing nighttime (minimum) temperatures are definitely absent only from July.

2.3.2.2. Precipitation

Total monthly precipitation, rainfall, and snowfall are given in Fig. 3. The mountain ranges of the western Cordillera, Baffin Island, and Labrador isolate central northern Canada from both Pacific and Atlantic moisture sources (Thompson, 1968: 266), and they channel continental air masses north and south over

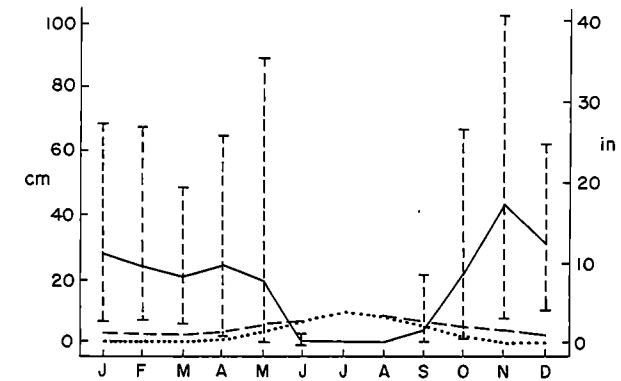


FIGURE 3. Mean monthly precipitation, rainfall, and snowfall. The dashed line (---) indicates the total precipitation for the winter months; the dotted line (....) monthly rainfall, which for the summer months is the total precipitation; and the solid line (—) represents total monthly snowfall. The vertical dashed lines indicate the range of the monthly snowfall values. Data from Big Trout Lake for the period 1939–1967 courtesy of the Atmospheric and Environment Service, Dufferin, Ontario.

the relatively dry interior (Bryson and Hare, 1974: 1; Hare and Hay, 1974: 52). For these reasons total annual precipitation in northern Ontario is small (about 60 cm). Most precipitation falls during the summer months from thunderstorms (Hare and Hay, 1974: 92). Total precipitation and the portion that falls as rain are distributed as shallow normal curves with a July peak.

Snowfall, in contrast, has a major peak in November and a secondary peak in April, both periods of shifting frontal zones and changing winds. Cool spring and late fall temperatures turn the tail ends of the precipitation curve into a large portion of the area's snowfall.

2.3.2.3. Wind

Wind direction and velocity are shown in Fig. 4. Prevailing winds in northern Ontario, especially during the winter, are from the northwest (Thompson, 1968: 269). During April and May, and into summer, wind direction is more variable due to cyclonic storms (Thompson, 1968: 262). Through the summer the warm south and southwest winds alternate with the cooler winds from the northwest, and by October the winter pattern again prevails.

In winter, light winds are common due to the dominance of arctic air. Wind velocities pick up in April and May, remaining elevated through the summer. The strongest winds occur during the transitional fall period, October and November.

The seasonal cycle of temperature changes and precipitation recorded at Muskrat Dam Lake in 1975 is shown in detail in Fig. 5. Day-to-day vagaries

Hay, 1974: 78–79; quoting McFadden, 1965). The interval between the first formation of ice and freeze-over averages about 19 days on rivers and 13 days on lakes, but both numbers are highly variable from location to location and year to year (Hare and Hay, 1974: 79; quoting Allen, 1964).

The spring thaw is relatively late in northern Ontario and Quebec. It reaches these southern areas at about the same time as it reaches the Yukon.* Hare and Thomas (1979) give three reasons for this: “the high frequency of arctic air-streams east of about 100°W; the extensive cloudiness that reflects back much of the solar radiation and the deep snow and ice-cover, which is highly reflective and hard to melt.” Hudson Bay has an influence, especially around its margins, but inland as well. In late spring the Bay is thawing or recently thawed. Its cold surface chills the lower air and induces thick ground fogs that inhibit solar warming (Savile, 1968: 407). Further, the Bay does not warm up sufficiently during summer to ameliorate the decreasing temperatures and early autumn frosts around its borders (Savile, 1968: 407).

Freeze-up and break-up dates for northern Ontario are shown in Fig. 6. Freeze-up can begin as early as 15 October, or as late as 13 November. It is preceded by the formation and melt of a full or partial ice cover. Break-up generally begins with a softening of the ice prior to the final thaw. The thaw itself may begin as early as 15 April or as late as 10 June, a range of 45 days.

A long series of break-up dates has been published by Moodie and Catchpole (1976) based on content analysis of diaries kept by Hudson’s Bay factors at Moose Factory and Ft. Albany, Ontario. Dates of first partial break-up at these locations for the period 1720–1870 are presented in Fig. 7. First partial break-up occurred at these sites any time between about 15 April and 20 May. These unique data chart the fluctuations of a physical factor which can be taken as a marker of similar variability in a biotic process quite important to humans—phenological spring.

2.3.3.2. Stream Flow

Because the topographic relief of the boreal forest is shallow and drainage slow, a precipitation-related change of several decimeters in the level of surface water can submerge or dessicate significant portions of the landscape. These areas are chiefly shallow lakes and streams, bogs, fens, and muskeg. This variation affects the behavior of fish, migratory waterfowl, and terrestrial animals, the possibility of fire, and the ease of movement of humans and animals.

Figure 8 shows seasonal and annual changes in the discharge rate of the Severn River. Observations in 1975 and conversations with residents suggest

* This same pattern apparently prevailed in the late Pleistocene, and was responsible for the fairly rapid melting of the Cordilleran ice sheet in northwestern Canada (Hare, 1976). This ice mass disappeared fully by 9000 years BP, while the Laurentide sheet lingered until perhaps as late as 5000 years BP in Keewatin and Labrador.

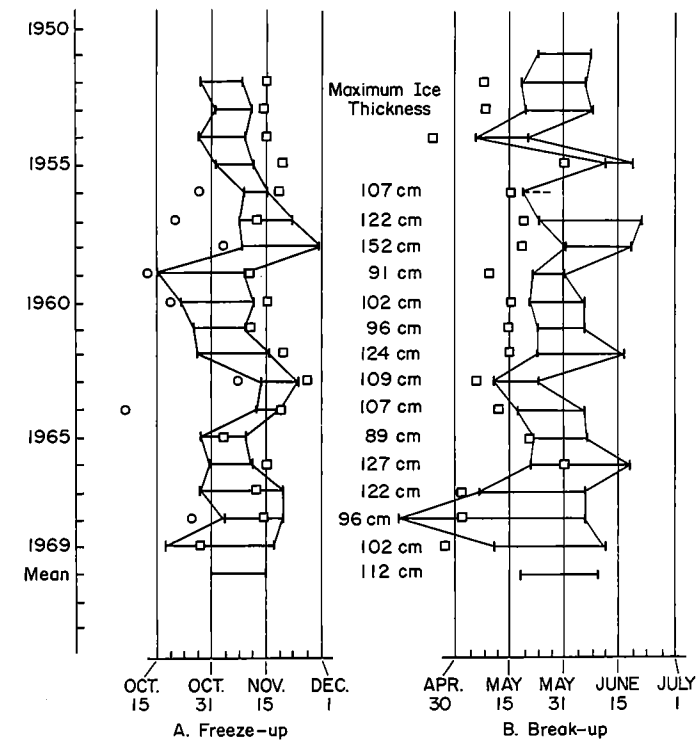


FIGURE 6. Freeze-up and break-up dates. (A) Freeze-up: Circles (O) indicate the formation of ice that later melted completely; horizontal lines (—) give the interval between the formation of the first permanent ice and complete freeze-over, excepting permanently open areas such as falls; squares (□) indicate that the ice became safe for light ground or air traffic. (B) Break-up: Squares (□) indicate the time at which the ice became unsafe for light traffic; horizontal lines (—) represent the interval between the earliest date of the final thaw of the season (definite ice melt, cracks, movement, or water puddles) and the disappearance of fixed or floating ice. Data from Allen and Cudbird (1971).

that this variability in flow causes changes of 1–2 m in the level of Muskrat Dam Lake. Stream flow is low in winter, rises in April and May (prior to break-up, because the headwaters and smaller tributaries of the southern river thaw early), peaks after break-up with the onset of summer precipitation, and drops in July and August to a plateau which is maintained until after freeze-up. Of special importance is the wide variability in monthly values from May through December.

2.3.3.3. Snow Cover

Snow is a surface feature affecting the movement and survival of humans, plants, and animals (Pruitt, 1970; Formozov, 1973). Its significance is more

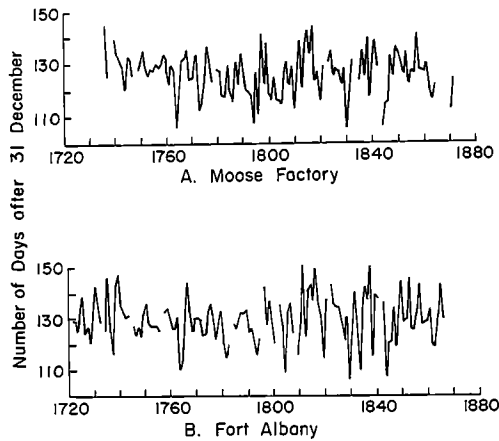


FIGURE 7. Historical dates of first partial break-up. The information to establish these dates was derived by content analysis of diaries kept by Hudson's Bay Company factors. After Moodie and Catchpole (1976). Copyright 1976 by The American Association for the Advancement of Science; used with permission.

readily appreciated if it is viewed as a cold, heterogeneous liquid, which covers the environment for up to 8 months of the year. It acts as shelter, home, or substrate to those organisms that have accommodated by living, respectively, beneath, within, or through or on top of it. Midwinter snow depths in northern Ontario average 60 cm. Year-to-year profiles show considerable variability (Fig. 9).

Snow accumulation begins in October, about the same time as freeze-up, continues to a peak in February, declines slightly in March, and falls quickly in April. Melting of the snow cover precedes break-up by a significant interval

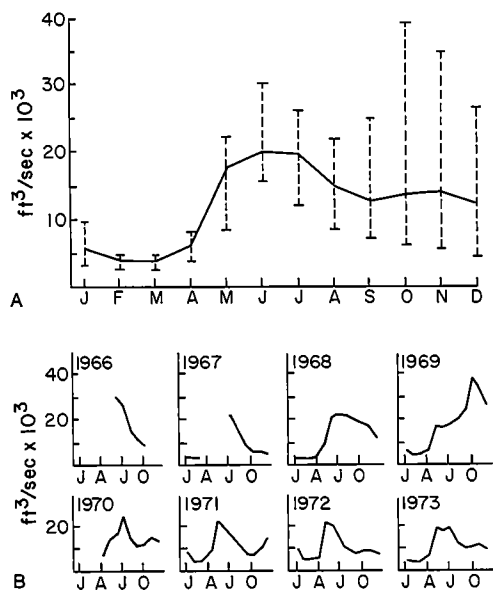


FIGURE 8. Annual variability in stream flow. (A) Mean monthly discharge for the period 1966-1973, measured at the outlet of Muskrat Dam Lake, on the Severn River. The vertical dashed lines show the range of monthly values. (B) Seasonal profiles for selected years. Data courtesy of the Water Survey of Canada, Department of Environment, Guelph, Ontario.

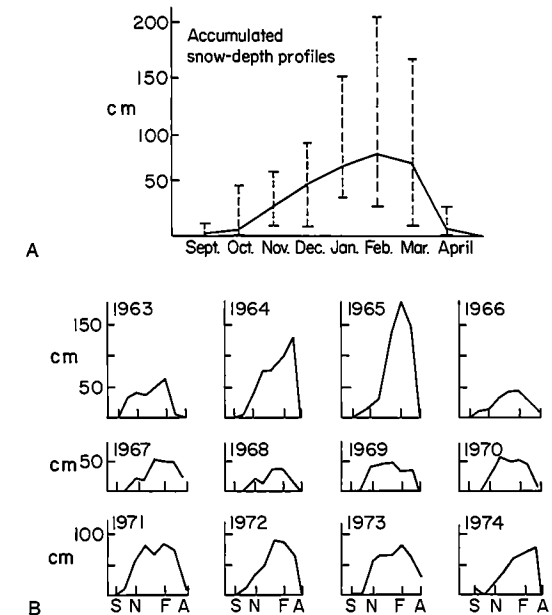


FIGURE 9. Annual variability in the accumulated snow depth profile. (A) Monthly mean snow depth for the period 1963-1975. The vertical dashed lines show the range of monthly mean values. (B) Seasonal profiles for selected years. Data from Environment Canada, 1963-1975, for Big Trout Lake, Ontario.

(Hare and Hay, 1974: 81). The large snowfall of April and May does not offset melting due to higher temperatures; high snowfall but decreasing snow depth indicates the general instability of the snow cover during this interval.

The interaction between ice formation and the initial snowfall accumulation affects freeze-up in ways important to humans. Both processes occur in late October or early November (Figs. 6 and 9). The best circumstance is for snowfall prior to or considerably after the beginning of freeze-up. If snow accumulates during the initial ice formation it can have either or both of two undesirable consequences: (1) a light snowfall on thin ice insulates it and retards or reverses the freeze-over process; and (2) a heavy or deep snowfall can settle or crack weak ice. Water seeps through and turns to slush in the snow. Either situation is hazardous, and both prolong the interval of limited mobility associated with freeze-up. These situations arise in the conjunction of two variable factors, and are consequently sporadic in occurrence.

One Cree-Ojibwa at Muskrat Dam Lake recalled an incidence of the second possibility in 1973:

The ice formed to about five inches. You could ride all over, even though there was no snow in the bush for trapping. Then about a foot of snow fell, and it turned into a mess of slush [on the lakes and rivers] . . . you couldn't go anywhere. (Anonymous, 1973)

The difficulties of travel applied equally to snowshoes and snowmobiles.

Snow depths are related to seasonal variations in precipitation and melting, but also vary among differing parts of the forest landscape. Snow is nearly always deeper in small openings, which receive fallen snow and snow that blows

from surrounding trees, than under the forest canopy, where branches intercept some of the snowfall (Kelsall and Prescott, 1971: 14). Snow is shallow on broad lakes and exposed uplands—anywhere that strong winds scour the surface—and deep along shorelines or in the lee of obstacles—anywhere that wind speed is reduced or wind deflected from the surface. Vegetation and topography thus interact to distribute fallen snow over the landscape.

Snow structure determines its density and hardness. This structure is the result of processes classified by Sommerfeld (1969) and described by LaChapelle (1969). Fallen snow crystals (“precipitated” snow) are diverse in history and characteristics, but share three attributes: complex structure, low density, and thermodynamic instability. These are basic to the changes subsequent to deposition that produce “metamorphosed” snow:

1. Equitemperature metamorphism results when snow crystals reduce their surface free energy by changing from complex forms to rounded particles of ice, through transfer of water molecules. This process is most effective at 0°C; it produces a settled snow of increased strength and density. Related changes caused by mechanical compaction or partial thawing and refreezing (collectively called firnification) can act to the same effect after this type of metamorphism ceases.
2. A second process, with a quite different outcome, is temperature gradient metamorphism. The temperature gradient between the relatively warm ground and the very cold air above the snow creates differences in equilibrium vapor pressure within the snow. As a result, water molecules migrate upward. This directional sublimation and deposition produces large, complex crystals, and a weak, low-density snow cover. “If the process is carried to completion, the snow develops a very fragile structure which will collapse into a cohesionless mass of crystals on slight disturbance” (LaChapelle, 1969: 18).
3. Finally, wind action hardens and compacts snow by abrading crystals into remnants that set together more easily. In addition, warm air or sun can thaw the snow surface, which forms a hard crust when refrozen (Pruitt, 1970: 86).

Of these processes, temperature gradient metamorphism dominates because of the continental climate of the boreal forest. It produces the weak snows of this area. Snow cover in northern Manitoba, for instance, is less dense by 2–3 times than that farther north (Arctic Archipelago) and farther south (northeastern U.S.) (Hare and Hay, 1974: 95, Fig. 19). Wind action on extensive ice-covered lakes and the wider rivers and on exposed topography produces a shallower and harder snow. Equitemperature metamorphism is more common in the spring, its effects augmented by temporary thaws, which produce a crust.

The interaction of fallen snow, vegetation, temperature, and wind results in a snow cover with localized surface differences that seasonally increase the heterogeneity of the boreal landscape.

2.3.4. Boreal Forest Vegetation

The boreal forest occupies Canada in a vast arc. From Newfoundland and central Quebec, it dips south of Hudson Bay and James Bay, and from there stretches north to the MacKenzie and Yukon regions. It is bordered on the north by the subarctic* and, in eastern Canada, on the south by the mixed forests of the Great Lakes and the St. Lawrence (Hare, 1950: 615; Rowe, 1972).

The relationship between boreal vegetation and climate has been long recognized. Hare (1950) related zonation of the eastern Canadian boreal forest to isopleths of potential evaporation, hence to the integrated effects of temperature and moisture. Bryson (1966) has shown that the northern and southern boundaries of the forest coincide with the modal position of the Arctic Frontal Zone in winter and summer, respectively (Fig. 1). Krebs and Barry (1970) confirmed the same relationship for the Eurasian boreal forest, and Larsen (1971) has demonstrated that air-mass frequencies are correlated with the distribution of many boreal plant species. In effect, the boreal forest corresponds to a particular climate. Although the direction and strength of causality for this relationship are not clear (Hare, 1968; quoted in Krebs and Barry, 1970: 548), it likely held in both glacial and postglacial times as well (Terasmae, 1973). One outcome of these relationships is that plant communities are more similar along the boreal arc, from Quebec into Manitoba, than along a much shorter north–south transect within any of the provinces (LaRoi, 1967; Larsen, 1972: 76–97).

These north–south differences are clear within the Severn drainage. The Lowland zone is made up almost exclusively of bogs, fens, and muskeg (Sjörs, 1959). Edaphic conditions on the Lowland are better than on the Shield, due mainly to the basic sedimentary rock substrate found there (in contrast to the more acidic granites of the Shield) (Ontario Department of Lands and Forests, 1963: 1; Hustich, 1957: 26–30). However, nearly level topography and poor drainage (Hustich, 1957: 26; Moir, 1958: 46) and unfavorable climate (Hustich, 1957: 26) limit the varieties of vegetation types growing in the Lowland area. To the south, on the Shield, the climate and the drainage are improved and the topography somewhat more diverse. Although the Shield has an edaphically poorer substrate, it supports a greater variety of vegetation habitats. The floras of the two areas are likewise quite different. Hustich (1957) collected at Ft. Severn on the northern edge of the Lowlands and at Big Trout Lake on the northern edge of the Shield and found only 25% of the species gathered common to both locations. This difference occurs over the distance of 275 km.

* The terms boreal and subarctic refer to different physiognomic and climatic zones, although sometimes they are used interchangeably. Subarctic refers to the transitional zone between the boreal forest and arctic tundra; it thus lies north of the boreal forest proper. For definitions and a concordance among northern zone terminologies, see Love (1970).

2.3.5. Vegetation Habitats

The boreal forest in northern Ontario contains a mosaic of vegetation habitats or patch-types (Fig. 10). These can be delineated following Ritchie's (1956, 1958, 1960) work in northern Manitoba, supplemented by personal observations and those of the botanists Hustich (1957), Moir (1958), and Sjörs (1959) in the Severn River drainage (Table 1).

The *closed black spruce forest* is found on drier uplands, those with moderate drainage. Black spruce is the dominant tree; saplings, shrubs, and herbs are scarce. A dense mat of feather mosses (Hustich, 1957: 21; Moir, 1958) covers the ground. This patch-type is a climax habitat. In the absence of disturbance it would dominate upland landforms.

Mixed spruce–aspen–birch forest occupies the same mesic landforms as the black spruce forest. It is a late seral community. Mature trembling aspen and white birch are being replaced by black spruce in the overstory. Shrub and herb layers have moderate abundances of species and individuals, providing a modest browse layer. Moir (1958) notes large tracts of this kind of forest in varying stages of succession in the Severn drainage.

The *aspen–birch forest* is a middle seral habitat, the first mature tree community of the upland successional sequence. The shrub and herb layers are similar to the mixed forest (above), but more dense. The regeneration of black spruce saplings and a ground litter of burned or unburned mature spruce usually provides evidence of fairly recent disturbance (Ritchie, 1956: 534). This patch-type provides an ample and well-stratified browse layer.

The fourth habitat is a *recent burn* or other disturbance. Overstory removal produces a vigorous regrowth of shrubs and herbaceous species. Trembling aspen is the commonest shrub, but jack pine and white birch can be present. The shrub layer includes various berries—velvetleaf blueberry, mountain cranberry, and bearberry—and willows. Herb species include abundant fireweed and pale cordalis. The lower browse layer is dense.

On outcrops of Precambrian rock *open jack pine forest* is the mature vegetation (Ritchie, 1956: 541). This habitat supports "a well developed mat of lichens on exposed outcrop surfaces" (Ritchie, 1956: 539), but it represents a limited portion of the Severn drainage (Moir, 1958: 65).

Lichen woodlands are notable because of their importance as caribou habitat, but they also are quite rare in northern Ontario. This vegetation type is made up of open tree stands, commonly black spruce, with a thick carpet of multihued *Cladonia* covering the intervening spaces (Hare, 1950: 622). This vegetation and its variants cover 60% of the Labrador–Ungava plateau (Hare, 1950: 622), but, in contrast, Moir (1958) fails to mention it in his Severn drainage survey, and Hustich (1957: 25) reports that lichen woodlands are scarce in the Big Trout Lake area. This near absence of lichen woodland in northern Ontario is probably due to the rarity of sites meeting the climatic, edaphic, and other requirements of the lichens themselves (Ahti and Hepburn, 1967: 26–29, 52). Lichens do best

TABLE 1. Structure, Composition, and Landform Associations of Northern Ontario Vegetation Types^a

Patch-Type A: Closed black spruce forest

Structure and composition: Sole canopy dominant: black spruce (*Picea mariana*). Uniform ground cover. Common shrubs: Labrador tea (*Ledum groenlandicum*), mountain cranberry (*Vaccinium vitis-idaea*). Common herbs: bunchberry (*Cornus canadensis*), horsetails (*Equisetum* spp.), tall lungwort (*Mertensia paniculata*), twinflower (*Linnaea borealis*), and sweet coltsfoot (*Petasites palmatus*). Ground cover a dense mat of moss; dominant species: *Pleurozium shreberie*. Reindeer lichens (*Cladonia* spp.) and mountain alder (*Alnus crispa*) occupy canopy gaps.

Landform: Upland, mesic. Well-developed mineral soil with moderate drainage. No evidence of recent fire or other disturbance.

Sources: Field observation. Ritchie (1956: 528–31), Moir (1958: 59–62), Hustich (1957: 21–23).

Patch-Type B: Mixed spruce–aspen–birch forest

Structure and composition: Canopy includes mature or senescing trembling aspen (*Populus tremuloides*) and birch (*Betula papyrifera*), being replaced by younger black spruce. Common shrubs: those of patch-type A plus mountain alder, speckled alder (*Alnus rugosa*), and diminutive willows (*Salix* spp.). Common herbs: those of patch-type A plus wild sarsaparilla (*Aralia nudicaulis*), pyrola (*Pyrola* spp.), and club mosses (*Lycopodium* spp.). Small canopy openings support strawberry (*Fragaria virginiana*), meadow rue (*Thalictrum venulosum*), and corn lily (*Clintonia borealis*).

Landform: Similar to patch-type A.

Sources: Field observation. Moir (1958: 62); similar to Ritchie (1956: 531–32).

Patch-Type C: Aspen–birch forest

Structure and composition: Canopy relatively open: trembling aspen and white birch. Shrub layer similar to patch-type B, but more dense. Common shrubs: those of patch-type B plus velvetleaf blueberry (*Vaccinium myrtilloides*), red currant (*Ribes triste*), rose (*Rosa acicularis*), and an occasional balsam fir (*Abies balsamea*). Common herbs: those of patch-type B plus dwarf raspberry (*Rubus pubescens*), fireweed (*Epilobium angustifolium*), and woodland strawberry (*Fragaria vesca*).

Landform: Similar to patch-type B.

Sources: Field observation. Moir (1958: 62), Hustich (1957: 25); similar to Ritchie (1956: 532–37).

Patch-Type D: Recent burn

Structure and composition: Tall shrub layer: trembling aspen, jack pine (*Pinus banksiana*), and white birch. Common shrubs: Speckled alder, mountain alder, willows, black spruce, velvetleaf blueberry, rose, and mountain cranberry. Common herbs: sweet coltsfoot, twinflower, fireweed, bunchberry, pyrola, aster (*Aster* spp.), goldenrod (*Solidago* spp.), Bicknell's cranesbill (*Geranium bicknellii*), and grasses and sedges.

Landform: Similar to patch-types A, B, and C.

Sources: Field observation. Rowe and Scotter (1973: 448–49); similar to Ritchie (1956: 537).

Patch-Type E: Open jack pine forest

Structure and composition: Open canopy of jack pine. Tall shrub layer sparse, including balsam willow (*Salix pyrifolia*) and white birch. Open outcrop surfaces support a dense mat of saxicolous lichens. Mesic crevices and depressions support lichens plus herbs and shrubs: velvetleaf blueberry, mountain cranberry, saxifrage (*Saxifraga tricuspidata*), three-toothed cinquefoil (*Potentilla tridentata*), fireweed, goldenrods, asters, sedges, and grasses. In drainage-imposed hollows: Labrador tea, black spruce, and mosses (most common: *Sphagnum* spp. and *Polytrichum commune*).

(continued)

TABLE 1. (continued)

Landform: Granitic outcrops (Precambrian) and ridges with little weathered soil, generally xeric.
Sources: Field observation. Ritchie (1956: 538–42), Moir (1958: 65).

Patch-Type F: Lichen woodland

Structure and composition: Open stands of black spruce, less frequently tamarack (*Larix laricina*) or jack pine. Shrubs and herbs rare. Ground cover a thick lichen mat, mostly reindeer lichens (*Cladonia* spp.).

Landform: Rugged topography or outcrops. Xeric, shallow soils.

Sources: Ahti and Hepburn (1967), Hare (1950). Air observations only were made during field work.

Patch-Type G: Muskeg

Structure and composition: Open stands of stunted black spruce. Discontinuous shrub layer: willows, dwarf birch (*Betula glandulosa*), alder, leatherleaf (*Chamaedaphne calyculata*), and Labrador tea. Herbs and prostrate shrubs: mountain cranberry, large cranberry (*Oxycoccus microcarpus*), cloud-berry (*Rubus chamaemorus*), sedges, and horsetails. Ground cover a thick, hummocky carpet of mosses, mostly *Sphagnum* spp.

Landform: Poorly drained depressions, flat, shallow, organic soils.

Sources: Field observation. Ritchie (1956: 547–49), Moir (1958: 62–65), Hustich (1957: 20–21), Ahti and Hepburn (1967: 455–47).

Patch-Type H: Peat bog

Structure and composition: Wet central part of bog: Marsh trefoil (*Menyanthes trifoliata*), marsh cinquefoil (*Potentilla palustris*), sedge (*Carex rostrata*), and cotton grass (*Eriophorum* spp.). Surrounding this a sedge-dominated community growing in a mat of submerged hypnoid mosses. Species include: sedges, false Solomon's seal (*Smilacina trifolia*), and chickweed (*Stellaria longifolia*). There is a third surrounding zone of hummocked sphagnum mosses, with bog rosemary (*Andromeda polifolia*), large cranberry, Labrador tea, leatherleaf, sweet gale (*Myrica gale*), bilberry (*Vaccinium uliginosum*), willows, cloudberry, goldenrod (*Solidago purshii*), and wild calla (*Calla palustris*).

Landform: Shallow wet depressions; hollows with peaty soils.

Sources: Field observation. Ritchie (1956: 549–51), Moir (1958: 74–75), Hustich (1957: 19–20), Ahti and Hepburn (1967: 43–49).

Patch-Type I: Aquatic vegetation

Structure and composition: (1) Shallow water bodies with gently sloping margins: in 50 cm to 1 m of water; pondweeds (*Potamogeton* spp.) and water-crowfoots (*Ranunculus* spp.). In less than 50 cm of water; bullhead lily (*Nuphar variegatum*), water smartweed (*Polygonum amphibium*), mare's tail (*Hippuris vulgaris*), and bladderwort (*Utricularia vulgaris*). In shallow margins, marsh trefoil, wild calla, marsh marigold (*Caltha palustris*), and sedges. (2) Deeper lakes, steeper shorelines: in 50 cm to 1 m of water; bullhead lily, pondweeds, bur-reed (*Sparganium angustifolium*), wapato (*Sagittaria cuneata*), swamp horsetail (*Equisetum fluviatile*), and sedges.

Landform: See above. Shallow (less than 1 m) margins of lakes, streams, and rivers, especially coves, stream confluences, or slow-flowing narrows.

Sources: Field observation. Ritchie (1956: 551–52).

Patch-Type J: Aquatic areas

This patch-type encompasses areas beyond the shore zones, which do not support emergent vegetation.

(continued)

TABLE 1. (continued)

Patch-Type K: Vegetation of lake margins

Structure and composition: Shrubs dominate at the water's edge: willows, sweet gale, mountain alder, and red-osier dogwood (*Cornus stolonifera*). Several meters inland is a tree stratum dominated by willow and balsam poplar (*Populus balsamifera*). Other species: white birch, tamarack, black spruce, swamp horsetail (*Equisetum fluviatile*), rose, strawberries, squashberry (*Viburnum edule*), wild sarsaparilla, and bunchberry.

Landform: Clay and stone shorelines along the water's edge.

Sources: Field observation. Ritchie (1956: 552–53), Moir (1958: 79–80).

*Plant identification by Sara DeGraff. Specimens on file at Bailey Hortorium, Cornell University, Ithaca, New York.

in cool to cold moist situations where soil or substrate conditions are poor. On wet substrates they are supplanted by muskeg and bogs and, where edaphic conditions are good, by vascular plants. The impeded drainage in northern Ontario, which favored muskeg development, was simultaneously detrimental to the spread of lichens.

Muskeg “describes a bog forest which has a single tree stratum of *Picea mariana*, and a hummocked ground vegetation of mosses—chiefly species of sphagnum—which bears a varied shrub and herb community dominated by *Ledum groenlandicum*” (Ritchie, 1956: 528; also MacFarlane, 1969). It is physiognomically differentiated from the peat bog in that the latter does not have a tree layer. Muskeg is fairly constant in its structure and composition over large areas (Ritchie, 1956; Moir, 1958: 65), and it occupies much of the Severn drainage (Moir, 1958: 62, 68; Hustich, 1957: 24). Relatively few vascular plants occur in this habitat, although in some cases the dry peaty surfaces of the raised hummocks support poorly developed *Cladonia* lichens (Ahti and Hepburn, 1967: 33–34, 46–47).

The *peat bog* is produced by a saturated accumulation of poorly decomposed organic matter. Usually a shallow central lake is surrounded by sequential zones of more mature bog vegetation. At the outer margin a bog often grades into muskeg; its shape is determined by the underlying mineral substratum (Sjörs, 1959: 3).

Two variations on the bog are the tamarack bog forest and the fen. In the tamarack bog forest (Moir, 1958: 66) tamarack replaces spruce as the tree dominant over a wet, muskeg-like surface. The fen has structural and compositional differences from bogs which derive from its water and nutrient source. A bog is highly acidic and derives most of its water from rainfall, poor in metal ions. A fen, in contrast, develops from a surface water source. This horizontal flow percolates through peat and mineral soil, and is richer in ions and is less acidic. Consequently, the fen supports a more abundant and varied flora (Sjörs, 1959: 3). The hummocks of a fen tend to be elongate across the axis of the water flow, so that from air they and the water-filled hollows form a striking laminar pattern.

Tamarack bogs and fens are common in the Severn drainage (Moir, 1958: 66, 74).

Due to fairly level topography and the gradual slope of many submerged areas adjacent to shorelines, bottom-rooted aquatic vegetation occupies a significant area. It is common in shallow coves, narrows between lakes, and at the broad confluences of slow-flowing streams or rivers.

Aquatic areas take in the lake and river areas beyond the shallow shorelines supporting aquatic vegetation.

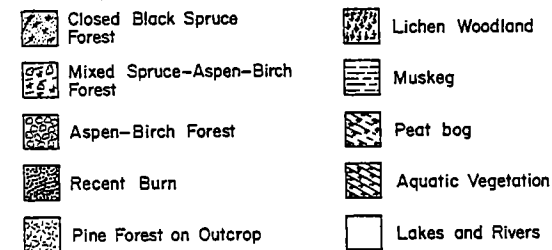
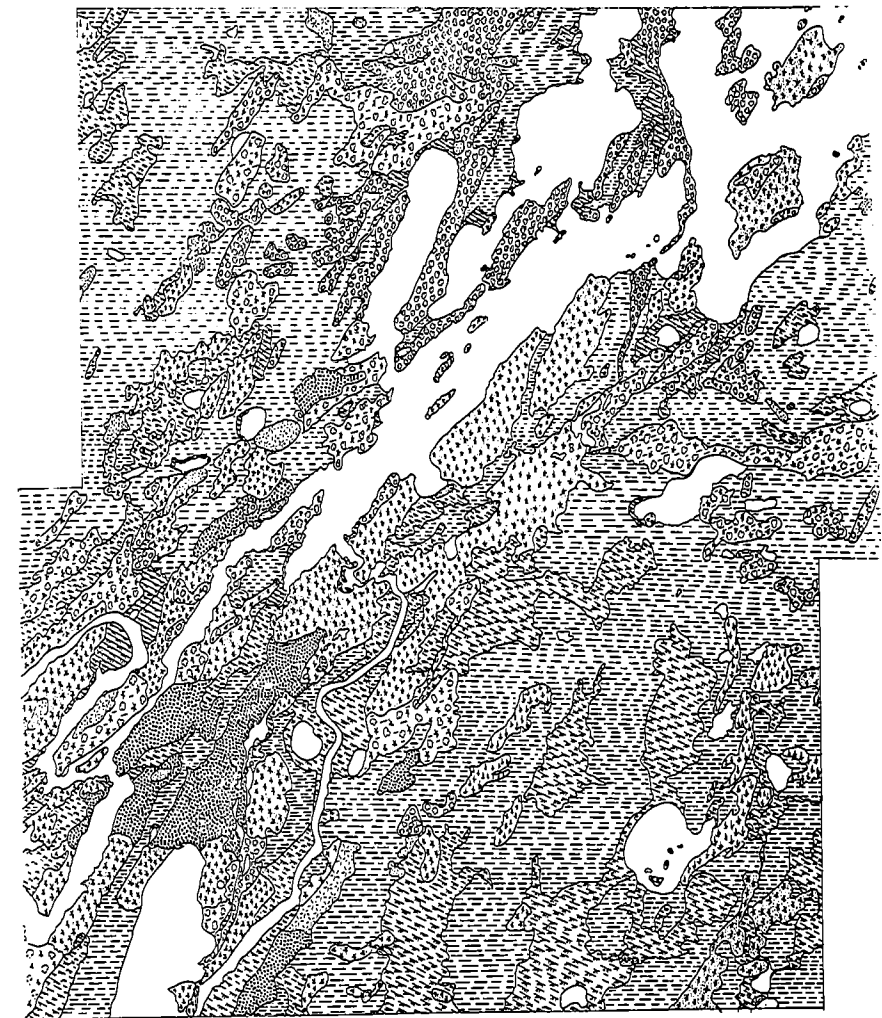
The *vegetation of lake and stream margins* is an ecotone. Often less than 10 m in width, this sinuous habitat is a ubiquitous feature of the northern landscape and it supports a productive and diverse plant community (Moir, 1958: 79).

2.3.6. Vegetation Patches and Dynamics

The distribution of these patches and quantitative aspects of their sizes and extent are evident in Fig. 10 and Table 2. Several things stand out. Patches are small, dispersed, and irregular in outline. Upland habitats are set into a matrix of muskeg and peat bogs. The latter two habitats and aquatic areas cover almost 70% of the surface. The remainder of the forest is predominantly various stages of the upland sere, from recent burns or other disturbances to closed black spruce forest. It should be evident that the complexity and small scale of this habitat mosaic make its use a matter of microgeography.

The habitat mosaic of the boreal forest is created partly by the associations of vegetation communities with edaphic and landform conditions, but it has an internal rhythm of disturbance and succession as well. The pattern evident in Fig. 10 is a dynamic one. Disturbance maintains the mosaic quality of the boreal forest, and gives the forest a short-term historical dimension. Three kinds of disturbance are important: snow, wind, and, especially, fire. In the absence of these factors black spruce forest would dominate upland sites, but the disturbances are endemic and recurrent features of the boreal ecosystem.

FIGURE 10. Vegetation patches. The definition and recognition of these associations is based on Ritchie's (1956, 1958, 1960) research in the Manitoba boreal forest, somewhat modified by field observations and by the work of the botanists Moir (1958) and Hustich (1957) within the Severn River drainage (Winterhalder, 1977: 128–148). A stereoscopic interpretation of black and white aerial photos (provided by the National Airphoto Library, Survey and Mapping Branch, Energy, Mines and Resources, Ottawa) was used in preparation of the map. The interpretation relied on (a) the author's familiarity with the area, (b) a series of low-level color aerial photos taken by the author at the autumn peak of vegetation color distinctions, which overlapped and could be correlated with the textural and tonal features of the high-altitude photos, and (c) reference to publications describing the preparation of similar maps of boreal forest vegetation (Larsen, 1962, 1972; Ritchie, 1958). Map prepared by Sarah DeGraff.



Scale in Kilometers
0 1 2 3 4 5

TABLE 2. Vegetation Patch-Types: Number, Size, and Proportional Area^a

Patch type	Number of patches	Mean size, ^b km ²	Total area, km ²	Percent of all area	Percent of upland (successional) area
A. Closed black spruce forest	74	0.73	53.9	12	39
B. Mixed spruce–aspen–birch forest	55	0.64	35.1	08	26
C. Aspen–birch forest	29	0.76	22.1	05	16
D. Recent burn	10	1.38	13.8	03	10
E. Open jack pine forest	17	0.14	2.4	01	03
F. Lichen woodland	13	0.53	6.8	02	06
G. Muskeg	38	4.24	161.0	37	—
H. Peat bog	57	0.99	56.4	13	—
I. Aquatic vegetation	38	0.20	7.6	02	—
J. Lakes and rivers:	1	63.10	63.1	14	—
Muskrat Dam Lake					
Others	54	0.30	16.4	04	—
Totals	386		438.6	101	100

^aFrom Winterhalder (1977: 145).

^bThe sizes of individual patches were calculated by placing a transparent point grid, calibrated on geometric shapes of known area, over the aerial photos used to prepare Fig. 10. A regression equation established the relationship between point counts for patches and their areas.

2.3.6.1. Snowthrow, Windthrow, and Fire

Qali, a Forest Eskimo term referring to the snow that accumulates on trees, is one agent initiating succession (Pruitt, 1958, 1970: 91). Low wind velocities allow the trunks of black spruce and other trees to accumulate *qali*. Birch and alder adjust by bending; spruce is not so supple. As long as the black spruce tree remains vertical it usually can accommodate the load. If the tree cants slightly, the *qali* will eventually break it and surrounding trees, until an opening forms that is large enough to allow the wind circulation that prevents further accumulation. Once a small *qali* opening is made, trees on its edge grow unevenly, leaning into the clearing. This produces a susceptible margin that grows until the enlargement is halted by air currents. With the spruce canopy removed and mosses stifled by dead spruce needles, deciduous vegetation occupies the clearing and initiates succession.

Blowdown, the toppling of trees by wind, is a related agent of disturbance (Ritchie, 1956: 528; Pruitt, 1958: 169). Because of the domino effect, the wind tends to throw a swath of trees.

Fire is probably the most important of these agents (Wright and Heinselman, 1973; Rowe and Scotter, 1973; Viereck, 1973). Evidence for periodic fires in northern conifer forests extends back as far as recording techniques can illuminate ecosystem history (Terasmae and Weeks, 1979; Wright and Heinselman, 1973:

320–321). For instance, Moir (1958) found charcoal fragments scattered through profiles dug in the muskeg surrounding Sandy Lake, indicating “fairly frequent” fires. Examining charcoal fragments incorporated into lake sediments in the southern boreal forest, Terasmae and Weeks (1979: 123) found a mean frequency of one fire every 95–100 years in the period from 8100 years BP to the present. In central portions of the core, coincident with the warmer and drier Hypsithermal climatic interval, the average period between fires in the area of the lake examined dropped to 48–56 years.

Forest vegetation tends to occur in small homogeneous patches which abut one another along abrupt and irregular boundaries (Ritchie, 1956: 532; Rowe and Scotter, 1973: 447). Commonly these boundaries are not associated with landform changes, and appear rather to be the margins of old burns.

Vegetation age also reflects fire disturbance. Northern conifer forests are young: in Canada less than 100 years old on average (Rowe and Scotter, 1973: 447) and in Alaska less than 150 years old (Viereck, 1973: 474), although small, usually insular, areas of older vegetation exist. These 100–150 year figures indicate that a given area will burn or suffer a similar disturbance on equivalent or somewhat shorter time intervals (Shafi and Yarranton, 1973a: 89).

The causes, frequency, and patterning of fires all have consequences for the forest mosaic. Although most fires in northern zones are caused by humans, away from population centers, the majority are lightning-started (Viereck, 1973: 470–71; Johnson and Rowe, 1975: 3). Lightning fires are concentrated in June and July, when thunderstorms are generated by the activity of marine Pacific air along the Arctic Front (Johnson and Rowe, 1975: 8). Fire danger is high, and fires occur in remote areas. Consequently, lightning fires account for the majority of hectares burned in the north (Johnson and Rowe, 1975: 4–5; Rowe and Scotter, 1973: 447).

The number of lightning fires started and the total area burned show large annual variability (Johnson and Rowe, 1975: 3). The meteorological origin of these fires ensures their dispersal. Further, most such fires are small. In northern Saskatchewan 88% of the areas burned are less than 41 ha, a figure which suggests “good reason for the patchiness of vegetation” (Rowe and Scotter, 1973: 452–53). In the long term, however, a relatively few large fires burn the greatest area:

But rarely do such conflagrations completely demolish the forest. Because of the vagaries of wind, and to some extent because of topography and the disposition of wetlands and water bodies, islands of undamaged vegetation often escape. In fact some students of fire believe that the forest patchwork pattern is as much due to isolated remnants in a burned matrix as to spot fires in an unburned matrix. (Rowe and Scotter, 1973: 453)

Either way the result is a mosaic of patch-types, even-aged and sharply bounded, small and irregularly dispersed.

2.3.6.2. Succession and Changing Productivities

Shafi and Yarranton (1973a, b) have studied changes in plant composition during postfire succession in northern Ontario boreal forest. They define four

seral states following a burn: (1) The initial heterogeneity, a result of uneven fire effects, lasts for 1 year. (2) The early phase, from 1 to 4 years, is one of relative homogeneity in which the vegetation is dominated by a few colonizing species. (3) Recovery of many species, a rapid growth in abundance, and renewed heterogeneity characterize the third phase, from 4 to about 15 years. (4) The late phase, from 15 to 50+ years, is again one of relative homogeneity. A canopy of black spruce dominates on wetter sites, jack pine or trembling aspen on the drier ones (Shafi and Yarranton, 1973a: 88). This succession occurs rather rapidly, the four stages concluding within about 50 years of the disturbance. This is habitat turnover on a scale commensurate with a human lifetime.

The functional ecosystem effects that accompany these composition and structural changes can be summarized, after Wright and Heinselman (1973: 324–25), as follows: (1) fire stimulates nutrient cycling and energy flow by releasing materials locked into slowly decomposing biomass; (2) fire creates the mosaic of different, but internally relatively homogeneous patch-types that occupy the landscape; (3) fire controls the scale of the forest mosaic, and increases regional diversity by maintaining a variety of microhabitats or vegetation communities; and (4) by maintaining vegetation diversity, fire over the long term contributes to forest stability (Loucks, 1970; Wright and Heinselman, 1973: 322).

The abundance and distribution of animal populations in the boreal forest are products of this dynamic mosaic, a point well summarized by Rowe and Scotter (1973: 457–58):

Faunal succession follows plant succession, and there are optimum habitats or stages of plant succession for every animal species. Therefore, inasmuch as fire initiates and terminates succession it exerts both short-term and long-term effects . . . the conclusion must be that any influence tending toward diversifying the landscape at large and small scales will increase the diversity of the fauna as well as the population density of some species. By maintaining a mosaic pattern in the boreal forest, fire assists in the maintenance of diverse wildlife populations.

2.3.7. Fauna

A description of the population characteristics, distribution, and behavior of the animals inhabiting the boreal forest would run to hundreds of pages, even if limited to topics immediately important to humans. A brief summary for two species—moose and hare—is given here. These two organisms provide a sense of the significant factors and they give some tether and detail to the more general observations which follow and which embrace the other important species.

2.3.7.1. Moose

The moose (*Alces alces*) is the largest extant member of the deer family. Adult male moose weight between 329 and 635 kg, adult females between 227 and 408 kg. The species is circumpolar in distribution; the subspecies inhabiting northwestern Ontario is *andersonii* (Peterson, 1966).

Moose are subject to large seasonal changes in body weight. Gasaway and Coady (1974: 228, 254) calculate a winter weight loss of 24% for breeding females in Alaska. Lent (1974: 310) indicates that males may lose 20% of their body weight during rut, while females lose no more than 5%. Much of this weight fluctuation involves high-calorie fatty tissue, making seasonal changes in energy value even greater than those of weight.

Based on aerial surveys of the Round Lake area, Addison (1971: 41) obtained a moose density of one animal/18 km². This estimate is similar to that of Brassard *et al.* (1974: 73) for a comparable habitat in Quebec, one moose/17 km², and somewhat below the “highest densities” found in Manitoba boreal forest, one moose/10 km² (Krefting, 1974: 84). Allowing for age structure, and averaging the weight of males and females, this estimate of one moose/18 km² results in a biomass of 17.2 kg/km².

Moose populations are known to vary in response to at least two major environmental factors—snow depth and habitat quality: “Moose populations everywhere fluctuate dynamically in response to environmental changes, and there are great local variations in abundance in time within the animals range. . . . Moose populations are constantly expanding or contracting” (Kelsall and Telfer, 1974: 117–18; see also Bishop and Rausch, 1974: 589). Bishop and Rausch give one example, from Alaska, of snow effects. In 1956 moose were abundant, with large winter aggregations on seral range. Severe snowfall (total 315 cm; depths up to 114 cm) in 1965–66 reduced the herd by 50%. The subsequent winter was less severe, but deep snow in the spring, when food supplies are low and the energy demands of pregnant females high, kept calf production low. The population recovered through 1968; in 1969 calves represented 23% of the animals. The winter of 1970–71 was again severe (snow depths approaching 101 cm) and again mortality approached 50%. The 1971 calf production portended fairly rapid recovery. Two crashes of this moose population within a 16-year period were related to snow conditions. The example also indicates the rapid recovery potential of moose. Snow depths such as these do occur sporadically in northern Ontario (Fig. 9), presumably with the same effect.

The creation of early succession habitats in maturing forest increases moose density, and populations fluctuate with changes in the frequency or extent of fires or other disturbances. In another Alaskan example, Cushwa and Coady (1976: 11) indicate that the moose populations increased about 400% during 1950–53 on 290,000 acres that burned in 1947 (see also LeResche, 1974: 409). Population growth can be rapid when there is a sudden favorable improvement in habitat. As with snow, fire represents a low-predictability factor determining moose population densities.

The ability to respond quickly to population depletion or habitat opportunities arises from the fairly high reproductive potential of the moose—20–25% (Simkin, 1974: 517). This can be traced partially to a behavior rare in ungulates, consistent twinning (Geist, 1974). Geist (1974) discusses the evolution of this

elevated reproductive potential, relating it to dynamic qualities of the boreal forest habitat, cold stress, and predation pressure.

Moose are adapted to consume a wide variety of boreal vegetation. Only a few species, however, are available and contribute to diet in quantity in winter (Kelsall and Telfer, 1974: 120–121). Willows and trembling aspen are major foods (Cushwa and Coady, 1976: 11). Tall shrub (Bishop and Rausch, 1974: 574) or shrub and deciduous tree communities (Cushwa and Coady, 1976: 11) are primary winter feeding areas for moose. In effect, “winter food profoundly influences distribution” (Kelsall and Telfer, 1974: 121; see also Brassard *et al.*, 1974: 763, 768). The association between shrubby (browse-abundant) habitats and moose distribution increases as growing snow depths restrict the range of the animal (Coady, 1974: 423; LeResche, 1974: 406; Telfer, 1970: 557–58, Fig. 3). Snow limits access to herbaceous and low woody browse, and the reduced productivity or dormancy of species that extend above the snow surface limits the availability and quality of what can be consumed (Geist, 1974: 531; Gasaway and Coady, 1974). Winter is a time of energy deficit. In response moose seek areas of prime foraging habitat and limit subsequent movement (Bishop and Rausch, 1974: 571, 575, 585–86; Brassard *et al.*, 1974: 73; Geist, 1974: 532; Peek, 1974a: 206).

Moose shift to summer ranges abruptly when snow melt exposes patches of bare ground (Coady, 1974: 426). During the spring and summer they inhabit “extensive wet bogs” (Bishop and Rausch, 1974: 565) or areas with “plenty of shallow marshy water” (Cumming, 1972: 21), and the diet broadens to include aquatic plants such as yellow pond lily, pondweeds, and horsetail (Cumming, 1972: 10; Peek, 1974a: 209; Krefting, 1974: 96). Moose do not frequent the floating bogs surrounding some lakes (Cumming, 1972: 21). Moose seek aquatic habitats to escape insects and heat (Kelsall and Telfer, 1974: 125; Peek, 1974a: 209), as well as to consume aquatic vegetation. In the fall the diet shifts back to the twigs and buds of characteristic winter food species.

The snow-induced mortality mentioned above is closely related to the chest height of moose. In adults or yearlings this is about 100 cm. At snow depths of 44 cm, movement is not impeded, but at 70 cm, movement is restricted, and at depths greater than 90 cm, it is curtailed sufficiently to endanger maintenance of an adequate diet (Coady, 1974: 422–23; Kelsall and Prescott, 1971: 18; Telfer, 1970: 557–58, Fig. 3). As snow depths increase, moose become confined to preferred habitats. For instance, Coady (1974: 431) reports that winter ranges of moose are about 2.33 km², compared to 14.0 km² in summer. In late winter this range can shrink to less than 0.41 km², and winter movements average less than 400 m/day.

Snow structure qualities such as density and hardness also influence moose movements (Kelsall and Prescott, 1971; Coady, 1974: 430). A hard crust is both a hinderance and a hazard, as the sharp edges abrade and lacerate the legs and feet of the animals.

The importance of fire to moose was discussed, but three additional points should be covered. How soon after a fire does habitat improvement attract moose? Deciduous growth can begin within months of a fire. In the Alaskan example cited earlier, moose population increases were apparent 3–4 years after the burn (Cushwa and Coady, 1976: 11). Peek (1974b) surveyed the response to a large burn in northeastern Minnesota and found a twofold and fivefold population increase in the first and second year, respectively, following the fire. These increases were due largely to immigration that began within 6 months after the fire. Second, how long is habitat quality elevated by disturbance? Kelsall and Telfer (1974: 122; also Cushwa and Coady, 1976: 11) conclude, based on Canadian experience, “Moose apparently prefer habitat less than 50 years old.” Thus, it is the early seral stages (Shafi and Yarranton 1973a, b), that are important: “As forest succession advances, the quality of the habitats and populations decrease accordingly because at maturity the boreal forest shades out the understory browse, and the overstory trees grow beyond the reach of moose” (Krefting, 1974: 81). Finally, it should be evident that fire can affect, more or less independently, either the density or the distribution of moose populations.

Moose are usually solitary animals, but two or more can be found together (Cumming, 1972: 13–14). Cows may be accompanied by calves for a year after the birth, and bulls may gather in groups of 2–5 during the rut. Moose are seasonally associated with home ranges, and are consistent from year to year in their use (LeResche, 1974: 401). These can be contiguous, or separated by up to 10 km. Particularly in winter, moose may move only several hundred meters a day (van Ballenberghe and Peek, 1971). In effect, they are quite sedentary animals (Kelsall and Telfer, 1974: 120).

A conspicuous behavior of moose is the rut, a fairly concise 2–3 week period in late September and early October during which the great majority of calves are conceived (Lent, 1974: 307). The rut can occur in a variety of habitats, but “. . . there seem to be desirable or traditional locations for rutting activity” (Lent, 1974: 308, 315), and a tendency to locate along waterways (Cumming, 1972: 21). Both the males and females vocalize: the males produce a low “grunt,” and females “a long, more or less quavering, moan,” which can be heard up to about 5 km (Lent, 1974: 313, 315). In addition, the males make considerable noise by thrashing about in the brush (Lent, 1974: 313).

2.3.7.2. Hare

The snowshoe hare (*Lepus americanus*) is the best known of the species with cyclic population changes (Keith, 1963; Meslow and Keith, 1968). Hare populations throughout the boreal forest fluctuate in a regular pattern with a recurrence of about 10 years. Long a subject of curiosity and investigation (Elton, 1942), the causes of this dramatic cycle have only recently been identified in a convincing manner, tied to long-term field evidence (Keith, 1974).

Hare populations can be described as persistent within a very broad neighborhood of values; they are highly unstable. Subjective estimates of peak abundance are divergent in reliability and results. Keith (1963: 73, 140) summarized published figures, which vary in northern areas from 1150 to 11,600 hare/km². The high estimate is one of the more reliable non-census figures. The highest estimate of peak density from an actual census is, however, 1300 hare/km². At low points in the cycle hare virtually disappear, and estimates have placed populations at less than one animal/km².

Based on 6 years of extensive field studies, beginning shortly after a population peak, Meslow and Keith (1968: 831) extrapolated backward to a conservative peak density of 511 hare/km² and measured the low point of the cycle to be 13 hare/km². In a later publication Keith (1974: 30) reported that this population eventually reached a second peak of 1120 hare/km². Two years later it had fallen to 147 hare/km².

Using 1150 and 13 animals/km² as estimates of high and low density, one obtains hare biomass fluctuation between 1610 and 18.2 kg/km².

There is a seasonal fluctuation in hare numbers not evident in these figures. Summer-to-summer survival rates of adult hare vary from a low of 13% during a population decline to 28% when the population is increasing (Meslow and Keith, 1968: 822). During the decline the mean annual number of young born for each female was 7.8, and during the population increase the number was 18 (Meslow and Keith, 1968: 825). Hare numbers swell during summer as litters enter the population and, depending on the point in the cycle, decline by 70–87% through winter.

On a continental level, recurrence of hare population cycles averages 9 years (Keith, 1963: 62–68). For the Hudson Bay watershed area recurrent peaks occur on intervals of 8–11 years. The fluctuations are synchronous over separated local populations, and more broadly, are synchronous on regional and on continental scales (Keith, 1963: 30, 58, 62; Bulmer, 1974). Hare population fluctuations are also more or less synchronous with those of grouse, ptarmigan, and lynx (Keith, 1963: 62). In contrast, muskrat numbers appear to fluctuate just opposite to those of hare (Bulmer, 1974: 705; cf. Winterhalder, 1980b).

Hare avoid mature woodlands in favor of bushier habitats, such as aspen with small bushy conifers, conifer swamps (especially those with small uplands of aspen), areas previously burned, alder swamps, and young jack pine areas (Bider, 1961: 93; Grange, 1932: 4, 13; Keith, 1966: 829). Their movement and distribution are patterned by these vegetational preferences in fall, winter, and spring, when they browse on twigs and buds (Bider, 1961: 87). In summer, however, the bloom of plentiful and widely distributed herbaceous vegetation reduces the association between hare and particular habitat types (Bider, 1961: 91).

The association of hare with specific habitats also changes in a regular manner with population. Hare occupy favorable habitats at low densities, but spread into less suitable ones at population peaks. Thus, during hare “shortages”

there are places of “local abundance” (Grange, 1932: 17), and Cox (1936: 217) notes that even at peaks of abundance some localities swarm with hare while in surrounding areas the lagomorph is only moderately numerous. Keith (1966: 828–29) studied the distribution of hare in Alberta boreal forest for three seasons of declining population. The hare population shrank from 629 to 36 animals, but the actual density in the occupied habitats contracted from 2.4 to 0.5 hare/ha, relatively less than the overall decline in numbers. The pattern of shrinking habitat use was clear: “the first sections devoid of hare had the least amount of brushy cover, and the last to retain hare had the most” (Keith 1966: 829). An extension of this study (Meslow and Keith, 1968: 819) showed that for a 4-year period the population declined 97% and occupied range shrank 91%. Thus density remained about the same in a much reduced area of habitat: “Cyclic species tend to persist in scattered nuclei of favorable habitat during periodic lows, and disperse from these into less suitable habitat as populations increase” (Keith, 1963: 99). This pattern is in addition to the seasonal one.

Hare prefer early seral habitats. The immediate effects of a fire on hare were studied by Keith and Surrendi (1971). These authors found no evidence of mortality directly or indirectly attributable to the fire. Hare temporarily withdrew from severely burned habitat, but in June of the year following the fire they were reoccupying these areas, and “by late summer hare runways were common and well used throughout this area” (Keith and Surrendi, 1971: 21). After a temporary emigration, hare were quickly attracted back into burned areas.

Because hare move on the surface even of the low-density snows of the boreal forest, they are not affected by snow depth *per se*. However, restriction of food supply by snow cover, even in desirable habitats, is an important winter problem for the animal. Hare can only browse to a height of about 45 cm (Bider, 1961: 91), but this range is extended as their snow “platform” accumulates and melts (Pruitt, 1970: 93). Hare browsing moves up and down the vegetation profile with the snow surface, a feeding space that is most productive if the snow increases and decreases steadily. Aberrations in the snow accumulation or melt can threaten survival.

Hare travel on well-worn pathways called runways. Although they can move on the snow surface (Pruitt, 1970: 89), runways packed to a depth of 6–7 cm are frequently used (Grange, 1932: 15; Bider, 1961). Runways in sphagnum moss are sometimes used summer after summer, wearing a deep trough (Grange, 1932: 15). Hare move over a daily home range of about 1.6 ha. Total home range for females is 2.8 ha, for males 7.3 ha (Bider, 1961: 99). In general they are sedentary animals (Meslow and Keith, 1968). Movement is strongly dependent on weather. Inclement conditions (rain and wind) and light greatly restrict the movement of hare (Aldous, 1937: 50; Bider, 1961: 89), and movement in open areas is restricted on clear nights (Aldous, 1937: 56). Thus, although hare move within a defined habitat, “climatic and physical factors dampen or activate movements within [that] home range” (Bider, 1961: 101).

Finally, Keith (1963: 96) has observed that when hare become abundant they typically become "tamer."

2.3.7.3. Major Resource Species

These sketches for moose and hare highlight some important properties of the boreal forest ecosystem. They point out interactions that make up the "effective" (Netting, 1971) human resource environment. These include: seasonal changes in population and weight; long-term population fluctuations, some arising from factors such as snow and fire; the spatial distribution of each species, arising from social interaction, habitat preferences, and patterns, or from other environmental components affecting location and movement such as snowfall; and peculiarities of behavior. The descriptions give specific instances of the effects on fauna of snow cover, stream flow, habitat dynamics, and other factors analyzed earlier. Ideally, sketches for individual species would be compared, so that overlap or the lack of it in changing patterns of abundance and distribution could be identified.

Table 3 summarizes the population characteristics of major resource species in northern Ontario. The discussion of moose and hare exemplifies the kind of information used in its preparation (Winterhalder, 1977).

Biomass estimates are listed with rough parenthetical (plus, minus) designations of the position of the estimate with regard to probable boundaries of persistence. Density is subject to the same consideration, although the parenthetical evaluations have not been repeated. The assessments of stability and recurrence are qualitative and relative designations. Early winter group size indicates the actual resource unit that one would expect to encounter during this season. Not shown, but of great importance, are the seasonal fluctuations in the biomass and density of some species (e.g., hare, muskrat, grouse).

Additional biomass estimates are given in Table 4. Taken individually, these are generally much below the biomasses of the major resource populations. The biomass of waterfowl, for instance, is restricted on the Shield. In the nesting phase, even in aggregate, they have a low density in the boreal forest [probably less than 5 kg/km² (Winterhalder, 1977; Bellrose, 1976)]. In the migratory phase waterfowl can be of moderate but transitory abundance. Density is dependent on the timing and synchrony of migrations and, for the geese and dabbling ducks, on high-water levels, which on the Shield forestall feeding stopovers during the fall (Macaulay and Boag, 1974: 14). Similar scarcity is not the case for some areas of the Lowlands and coast, where the harvest and storage of migratory waterfowl was important both to native peoples and to fur trade personnel (Honigsmann, 1948; Hurlich, personal communication). Waterfowl follow fairly confined migration corridors (Bellrose, 1976), resulting in regional unevenness in the distribution of migratory populations. The diversity of nesting species decreases north of the Shield. But those species present are "frequently found in

TABLE 3. Population Characteristics of Major Resource Species^a

	Biomass, ^b kg/km ²	Density, animals/100 km ²	Stability	Recurrence	Early winter group size
Moose	17.2 (+ -)	5.6	Moderate	Irregular, short-term	680 kg (+ -), 1.8 individuals
Caribou	0.7 (+ -)	0.5	Moderate	Irregular, long-term	900 kg (+ -), 6 individuals
Beaver	20.9 (+ - -)	185	Moderate	Irregular, short-term	100 kg (+ -), 5 individuals
Muskrat	34.2 (+ + - -)	3,800	Low	Cyclic, 10 yr, irregular	0.9 kg, 1 individual
Hare	1,610-18.2	115,000-1,300	Low	Cyclic, 10 yr	1.5 kg, 1 individual
Ruffed grouse	54.0-6.0	8,600-1,000	Low	Cyclic, 10 yr	1.8 kg (+ -), 3 individuals
Spruce grouse	18.5-low	3,090-low	Low	Cyclic, 10 yr	1.8 kg (+ -), 3 individuals
Fish	675	—	High	—	—

^aFrom Winterhalder (1977: 275), with modification.

^bThe plus and minus signs in parentheses are meant to indicate especially broad upper and lower boundaries of persistence relative to the estimate. The summary parameters used in this table (e.g., persistence, stability, and recurrence) are explained in Winterhalder (1980a).

TABLE 4. Biomass and Density Estimates of Selected Boreal Forest Organisms^a

	Biomass, kg/km ²	Density, animals/100 km ²	Notes
Wolverine (<i>Gulo gulo</i>)	0.03–0.06	0.2–0.5	Scandinavian estimate, probably representative of Canada (van Zyll de Jong, 1975: 432, 434); weight from Banfield (1974: 332)
Wolf (<i>Canis lupus</i>)	0.72	2.3	Northern Minnesota
	0.24	0.8	Alaska
	0.94	3.0	Northwest Territories
	0.20	0.6	Saskatchewan (quoted in Mech, 1966: 47); weight from Mech (1966: 35)
Lynx (<i>Lynx canadensis</i>)	0.96–0.22	10.0–2.3	Northern Alberta; Cyclic high and low density from 8 years of annual census data (Brand <i>et al.</i> , 1976: p. 419, Table 1); weight from Banfield (1974: 349)
Marten (<i>Martes americana</i>)	0.80	96.5	Central Ontario (Francis and Stephenson, 1972: 2, 33–35); weight from Banfield (1974: 316)
Small mammals (four species, vole squirrel, and shrew)	109.0	—	Alaskan taiga; the figure represents a partial accounting of small mammals in the boreal forest; from Grodzinski (1971: 246)
Migratory passerine birds (17 species)	10.3	—	Boreal forest (Carbyn, 1971: 59, Table 3)

^aAdapted from Winterhalder (1977: 263–264).

in very great numbers at restricted localities” (Cooch, 1968: 453). Cooch gives an example of a nesting area of geese at Bowman Bay which supports 930 birds/km² (for a localized biomass of over 3200 kg/km²).

Table 5 summarizes the association between major resource species and patch-types. This table also notes the effects of climatic factors on these associations. These patches identify a localized area within the overall landscape mosaic where the likelihood of finding a particular species is greatest.

2.3.8 Energy and Snow

The ultimate limitation on energy flow at high latitudes can be traced to a reduced solar energy budget (MacPherson, 1968: 466). The available solar energy is concentrated in summer, and high albedo (reflectivity) of the northern land-

TABLE 5. Habitat Associations of Major Resource Species^a

Resource	Patch- or vegetation-type association	Notes
Moose		
Winter	Aspen–birch forest; recent burn; lake margins	Deep snowfall strengthens winter patch association
Summer	Aquatic vegetation; lake margins	Low water, heat, and insects strengthen summer patch association
Caribou		
Winter	Closed black spruce forest; pine forest on outcrop; lichen woodland	Deep snowfall strengthens winter patch association, especially for open jack pine forest
Summer	Peat bog	—
Beaver	Aquatic vegetation; lake margins	—
Muskrat	Aquatic vegetation	—
Hare		
Winter	Aspen–birch forest; recent burn	Association with specific patch-types increases during fall, winter, and spring, and when populations are low
Summer	Various	—
Ruffed grouse	Aspen–birch forest; recent burn; lake margins	—
Spruce grouse	Closed black spruce forest; spruce–aspen–birch forest	—
Fish	Aquatic vegetation; open water	Association with the shallow water habitat is influenced by temperature and increases in spring and fall and with spawning

^aFrom Winterhalder (1977: 277).

scape through the winter reduces solar warming significantly. In the spring a great deal of the energy influx is absorbed to melt snow and ice, and is therefore unavailable for life processes. This early spring period is doubly limited because a good part of the annual radiation budget falls while temperatures remain too low to allow transpiration and photosynthesis (Hare and Ritchie, 1972: 358).

The long-term result of this is a (relatively) impoverished flora—in genera and species—particularly in the tree stratum. A few hardy species of spruce, pine, larch, and fir, and hardwoods such as birches, poplars, willows, and alders, are the only representatives (Hare and Ritchie, 1972: 335). Surface energy and moisture availability have their greatest impact on zonal structure of the vegetation (Hare and Ritchie, 1972), producing the physiognomic changes—from closed black spruce forest to the open subarctic woodlands to arctic tundra—as

one moves northward. Productivity is restricted to a brief "bloom" during summer (Grodzinski, 1971: 236), and for the remainder of the year the quantity is limited, partly because vegetation is partially or wholly covered with snow. In addition, its nutritional quality is reduced due to dormancy (Aleksiuk and Cowan, 1969b: 471; Gasaway and Coady, 1974).

Table 6 summarizes plant biomass (phytomass) and net productivity of northern zones. From north to south the Severn River drainage probably spans the range of the values given.

The effects of limited primary productivity are expressed throughout the food chain in relatively low species numbers and low densities of extant animals (MacPherson, 1968: 466–67):

The small amount of new plant growth produced each summer, and available for forage, and the lengthy annual period during which plant food reserves are not added to, but can only shrink undoubtedly play important roles in limiting the abundance and diversity of the northern mammalian faunas. (MacPherson, 1968: 472)

Herbivore populations, swollen with the summer's births, decrease in density (and biomass) throughout the winter, due to slow depletion of vegetation food resources and endogenous reserves, weather-related mortality, and steady depredation by predators. Early spring is a difficult period for many species and the dietary overlap evident among the browsing animals suggest fairly strong resource competition during this period (MacPherson, 1968: 476; Wolfe, 1974). As with vegetation, the fauna of the boreal forest should not be viewed as a finely tuned or stable community on the "harmony and balance in nature" model. Energy limitations and cold enhance the importance of snow in two ways: as an insulating medium, and as a substrate. Small mammals live in the subnival zone and are dependent on snow insulation for survival (Pruitt, 1957, 1970: 86–87). The species that enter dens and a state of lethargy for the winter (MacPherson, 1968: 476) also benefit from snow insulation. The semiaquatic species spend much of the winter beneath snow-covered ice. Mink, for instance, frequent the dry under-ice margins of streams (MacPherson, 1968: 478). The larger mammals stand through the snow, and suffer the energy costs of wading in it. In contrast, the snowshoe hare and the lynx live on the snow surface; they are "floaters"

TABLE 6. Boreal Forest Phytomass and Productivity^a

Boreal zone	Phytomass, tonnes/ha ^b	Net productivity, tonnes/ha per yr	Pr		
			Pr ₁	Pr ₂	Pr ₃
Forest-tundra and woodland	50–150	3–5	1	0.3	2
Forest	200–400	5–10	1–1.5	0.5	2

^aFrom Hare and Thomas (1979: 125). Definitions of conversion efficiencies quoted: Pr₁, percent conversion of net radiation per annum; Pr₂, percent conversion of global solar radiation per annum; Pr₃, percent conversion of photosynthetically active radiation received when air temperature is 10°C or above. Used with permission.

^bTonne = 1 metric ton = 1000 kg.

(Pruitt, 1970: 89). The only species that escape this classification based on habits relative to the snow surface are those that migrate, mainly avifauna. Humans, with the aid of snowshoes, have followed the lead of the hare and the lynx and have adopted the role of floaters.

2.4. Discussion and Conclusion

The boreal forest presents a dramatic and unusually well-documented case of what is probably common to most environments: (1) dynamic patterns of spatial heterogeneity in the landscape and in dispersion of animal populations, and (2) recurrent fluctuations in the population density of flora and fauna. These fluctuations are more or less weakly synchronized because of the interlocking effects of food chains and overlapping responses to environmental factors such as climate. They are more or less regular in their patterning. This environment defies characterization in normative terms: repeatedly the words variation, fluctuation, dynamic, or change have been used to capture its properties. In this discussion I will note some terms and concepts which can be applied in summarizing these nonnormative properties. Environmental analysis has generally not kept pace with the growing sophistication of models available for relating human adaptations to environmental factors (Winterhalder, 1980a). The boreal forest provides a good context for beginning to correct this.

Normative analysis diverts attention from the significant properties of the boreal habitat. The 10-year average number of snowshoe hare has a mathematical meaning, but it is an abstract and ephemeral value without substance for events in the forest. The same can be said for phenomena from temperature to carrying capacity. Nor are averages particularly relevant to adaptation. Organisms that prey on hare, for instance, must adjust to surfeit, superabundance, and rapid transitions between the two, not to an average. Figure 5 makes apparent the difference between daily temperature ranges and monthly means of the same high and low values. Adaptations are structured around the conditions organisms *actually* encounter. Those conditions cover a range of values and may have their greatest impact toward the end points of that range.

For most theoretical and practical purposes the remedy of an extensive and highly detailed description of forest ecology is not useful or feasible. Selectivity and summary parameters—"sufficient parameters" (Levins, 1966)—are required.

Selectivity is the harder point to generalize about. It is difficult to know in advance which factors or properties of an environment have a significant impact on human adjustment. For instance, it was rather late in a study of foraging behavior (Winterhalder, Chapter 6, this volume) that the importance of stream flow in the boreal forest became evident. Even for a factor of obvious importance, such as cold, close field work may be necessary to determine the actual manner and timing of its effects (Hurlich, Chapter 5, this volume). Further, some adaptively important phenomena do not emerge directly from an ecological survey;

they may arise from particular human interactions with the environment (Steegmann, Chapter 7, this volume; Morano, Chapter 8, this volume). Environmental analysis, then, does not provide an ecological background from which adaptive study begins. It is a continuing part of the research. The early placement of this chapter, and similar organization of other collections (e.g., Baker and Little, 1976) contains, then, a small chronological fib: the ecological description precedes the adaptation analyses, but its content was selected partly as a result of those analyses.

Sufficient parameters have been employed here to summarize spatial and temporal properties of the boreal environment. Spatially the most important terms have been patchiness or "grain" (Wiens, 1976). Analysis has focused on the small-scale spatial heterogeneity of the boreal forest. The interactions among landforms and soils, climatic factors (including those affecting the distribution of snow, ice, and water), vegetation associations and dynamics, and the dispersion of animal populations create a complex and sharply defined mosaic. This mosaic of patch-types is a microgeography of resources, hazards, and conditions which impede or facilitate human activities. It is a patchwork of highly localized adaptive situations, one always in flux. The anticipation of small-scaled grain may well be a valuable guide in the analysis of other environments.

Temporal properties of the forest have also been described with a set of sufficient parameters: stability, recurrence, and persistence among them [see Winterhalder (1980a) for a summary of these concepts]. Hare populations, for instance, can be characterized as unstable but resilient (Holling, 1973); unstable because they fluctuate markedly, resilient because even with extreme fluctuations hare populations maintain the same basic relationship to other aspects of the environment. They manage to persist in spite of drastic changes in abundance. Some other biotic components in the forest can be summarized this way.

Amplitude, frequency, and regularity are additional properties of time-varying factors. Botkin and Sobel (1975) have defined terms for these properties, and have argued cogently for the use of history-sensitive terminologies in ecological analysis. The population of a species (or some other variable) can be represented over time as a varying curve. The highest and lowest points over a long period are taken as the *boundaries of persistence* for that variable. The distance (or duration) until the curve repeats is defined as an interval of *recurrence*. These concepts describe a fluctuating variable without assuming it has an equilibrium value. Regularity is more difficult, but Colwell (1974) has defined a simple, quantitative technique for analyzing this property (which he calls predictability). This technique has not been applied here, although qualitative assessments of regularity have been given.

Using these terms (see Table 3), one can characterize hare populations as highly unstable, persistent within wide boundaries, and predictably recurrent (cyclic) on an interval of 10 years. Moose populations are persistent within narrower boundaries, moderately stable, and recurrent on irregular intervals. For moose those intervals are systematically determined by reproductive potential,

and by variability in snow depth and fire frequency acting through winter mortality and habitat conditions. Table 3 contains additional information on other species, and demonstrates that summary of temporal properties is possible without the distorting effects of averages. Although the dynamic temporal properties of the boreal forest are unusually clear, the same situation may characterize other environments as well.

Although it is tempting, there is some danger to understanding and little theoretical advantage in trying to briefly summarize the boreal forest as a whole. If it is called an unstable habitat, fish populations become only the first exception. If it is called a recurrent habitat, the postglacial development of muskeg stands out to belie the description. Accurate synthesis here (and perhaps in other environments) comes in a slightly different and not so telescoped form. Important components and processes can be summarized with appropriate concepts, and interactions among components can be traced in ways that make their effects on one another systematically predictable. This is less compact and somewhat more demanding than a normative portrait, but the extra effort is certainly the due of the forest and its inhabitants, and it is essential to understanding of human adaptation.

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3

Prehistory of the Interior Forest of Northern Ontario

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3.1. Introduction

The accumulation of a body of information upon which to base the reconstruction of the prehistory of the first people to occupy the boreal forest of the Precambrian Shield has been limited. The nomadic lifestyle of the original inhabitants has resulted in small, scattered archaeological sites. These sites have frequently been subjected to destruction by water inundation, dense forest invasion, and acidic soils; consequently, they yield comparatively sparse recoveries. They tend also to be concentrated in ecologically favorable locales, with the result that they have superpositioned deposits, frequently of an equivocal nature. Often hundreds of years of human activity are compacted into a depth of only a few centimeters. Further, the inhospitable and often inaccessible terrain of the interior forest has not, until recently, been attractive to archaeological investigators. Now, based on recent, extensive surveys, information is sufficient to make observations on the archaeological sequences of the cultural history of the original inhabitants (Dawson, 1976a, b; Dickson, 1972; Dewdney and Kidd, 1967; Hlacy, 1970, 1971; Kenyon, 1961; Koezur and Wright, 1976; Mayer-Oakes, 1970; Nash, 1970; Pollock, 1975, 1976; Pollock and Noble, 1975; Ridley, 1956, 1958; Tomenchuk and Irving, 1974; Wiersum and Tisdale, 1977; Wood *et al.*, 1976; Wright, 1967, 1968a, b, 1972a). The observations exclude the Hudson Bay Lowland, which, except for the Hawley Lake area (Pollock and Noble, 1975), appears to have been virtually unoccupied in prehistoric times (Dawson, 1976a; Wood *et al.*, 1976; Wright, 1972b).