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Ecological Sustainability of Birds in Boreal Forests

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ABSTRACT

We review characteristics of birds in boreal forests in the context of their ecological sustainability under both natural and anthropogenic disturbances. We identify the underlying ecological factors associated with boreal bird populations and their variability, review the interactions between boreal bird populations and disturbance, and describe some tools on how boreal bird populations may be conserved in the future. The boreal system has historically been an area with extensive disturbance such as fire, insect outbreaks, and wind. In addition, the boreal system is vulnerable to global climate change as well as increasing pressure on forest and water resources. Current knowledge indicates that birds play an important role in boreal forests, and sustaining these populations affords many benefits to the health of boreal forests. Many issues must be approached with caution, including the lack of knowledge on our ability to mimic natural disturbance regimes with management, our lack of understanding on fragmentation due to logging activity, which is different from permanent conversion to other land uses such as agriculture or residential area, and our lack of knowledge on what controls variability in boreal bird populations or the linkage between bird population fluctuations and productivity. The essential role that birds can provide is to clarify important ecological concerns and variables that not only will help to sustain bird populations, but also will contribute to the long–term health of the boreal forest for all species, including humans.

INTRODUCTION

The northern boreal forest, or taiga, an area dominated by forests, peatlands, and water, is one of the largest and youngest biomes in the world (Shugart et al. 1992, Helle and Niemi 1996). The current condition of the boreal forest varies from areas that have received intensive management for wood production (such as in northern Europe and Canada) to large, pristine forest areas that have never been logged (such as in central Siberia and in Alaska). The dominant natural disturbance of the boreal forest is fire (Heinselman 1973, Zackrisson 1977, Wein and MacLean 1983), although insect outbreaks, wind, and other animals (e.g., beaver, *Castor* spp.) are also significant disturbances in many areas (Pastor et al. 1996).

Boreal regions are expected to experience the greatest change in climate worldwide, due to global warming (Pastor et al. 1996). Because boreal regions contain huge pools of the world's carbon, climate warming in these regions may change them from a carbon sink to a carbon source (Post 1990, Pastor et al. 1996). Climate change can be viewed as a large, long–term stress on the boreal system, but logging is currently the primary human–induced disturbance influencing change in boreal forests. Land cover in boreal regions such as in Canada is undergoing massive change as a result of forestry operations, primarily the removal of trees over vast areas. Vitousek (1994) suggests that land use/land cover change and loss probably represent the biggest component of global change, with profound effects on biological diversity.

Our focus here is to increase our understanding of "Sustainability in Boreal Regions," the results of a workshop held at Lake Itasca State Park, Minnesota, United States (this issue). Specifically, we focus on boreal bird populations as one aspect of the boreal system to be sustained, and also on the role birds play in sustaining the boreal system.

The objective of the paper is to identify the important factors that influence and indicate sustainability of boreal bird populations. Here, "sustaining" embodies the concept of "sustainable development," in which development meets present and future human needs without damaging the environment and biological diversity (Lubchenco et al. 1991). We are interested in presenting the underlying ecological factors that will maintain and conserve boreal bird populations into the future or, theoretically, in "perpetuity," in the face of both natural and anthropogenic disturbances. Sustainability here refers to a variety of characteristics of bird populations, including the conservation of viable populations of all extant, indigenous species; the maintenance of inherent population variability; and, to the extent possible or realistic, the preservation of species composition and variability within boreal forests. We will: (1) characterize the boreal bird community, (2) identify possible underlying ecological factors associated with boreal bird populations, variability, and their trends, (3) describe what is known about the interactions between boreal birds and disturbance, and (4) review some tools that would be useful for sustaining boreal bird populations in the future.

Boreal bird communities

A considerable body of literature exists on boreal bird communities, including studies of life history and ecology for many species (e.g., Godfrey 1966, Erskine 1977, Welsh 1987, Haila and Järvinen 1990, Helle and Mönkkönen 1990, Helle and Niemi 1996, Kirk et al. 1996, Welsh and Lougheed 1996, Mönkkönen and Viro 1997, Niemi and Hanowski 1997, and Birds of North America series, Poole, Stettenheim, and Gill, editors). In general, birds constitute the majority of the terrestrial vertebrate species in most boreal communities. For instance, birds represent about 70% of all terrestrial vertebrate species in the Superior National Forest of northern Minnesota, United States, where Green (1995) documents 155 bird species, 52 mammal species, and 18 herpetofaunal species. In the western boreal forest of Canada (west of the Ontario–Manitoba border),

approximately 81% of terrestrial vertebrates are birds (Smith 1993). In the boreal forest of northeastern Ontario, birds represent approximately 71% of the terrestrial vertebrate species (D'Eon and Watt 1994). In Finland, birds make up about 75% of the terrestrial vertebrates. Within the boreal zone, there are about three times as many bird species as mammal species over the Holarctic region (Mönkkönen and Viro 1997). In general, the number of mammal, reptile, and amphibian species declines toward the north, so the proportion of the terrestrial vertebrate community consisting of bird species remains either relatively the same, or usually increases from south to north in the boreal forest.

The breeding boreal bird community is made up of three different groups: permanent residents, short–distance migrants (wintering in temperate areas), and long–distance migrants (wintering in the tropics). The proportion of migratory species in these communities varies considerably, depending on latitude and habitat type; however, the number of migratory species generally exceeds the number of permanent residents. For example, Helle and Niemi (1996) reported that permanent residents represent only 5–15% of the local breeding bird species. The numbers of long–distance migrant species tend to vary from about 30% (Haila and Järvinen 1990) to >50% (Helle and Niemi 1996) in many Nearctic boreal bird communities. More than 80% of all bird species breeding in the boreal region of Canada winter farther to the south, and approximately 50% winter in tropical or subtropical regions (Erskine 1977). In Fennoscandia, about 30% of the land bird species and 40% of individuals winter in the tropics, whereas 45% of land bird species and 48% of individuals, respectively, are classified as short–distance migrants.

Evidence for the importance of birds in a healthy forested ecosystem is increasing. In summer, most forest birds eat insects, especially phytophagous lepidopteran larvae. Several studies have shown that birds reduce insect densities (Holmes et al. 1979, Atlegrim 1989), especially when the insect populations are at either low or endemic levels (Crawford and Jennings 1989, Holmes 1990, Torgerson et al. 1990). Holling (1988) reported that bird predation of spruce budworm (*Choristoneura fumiferana*) could lengthen the time between budworm outbreaks. Although not in a boreal setting, Marquis and Whelan (1994) conducted exclosure experiments on oaks in Missouri, United States, and showed that predation by birds had a significant and positive effect on tree growth. They concluded that declines in North American populations of insectivorous birds may reduce forest productivity, because they would result in higher numbers of leaf–chewing insects that have negative effects on tree growth. Folke et al. (1996) reported that a 50–70% decline in Neotropical migrants would probably result in major changes to the tree species composition of the boreal forest. In one of the few economic studies on monetary benefits of bird predation, Takekawa and Garton (1984) estimated that bird predation on western spruce budworm (*Choristoneura occidentalis*) resulted in $1,820 (U.S. dollars) of positive economic benefit per year per square kilometer.

In addition to impacts of insectivorous birds, predatory birds have major influences on small–mammal populations, with ultimate effects on forest regeneration and health. For example, Korpimäki (1993) and Korpimäki and Krebs (1996) present evidence on the controlling influence of predatory birds on vole population cycles, especially in northern Fennoscandia. There are a variety of other ecosystem services that birds provide, including dissemination of seeds, nutrient and energy cycling, and predation of insects during nonbreeding seasons (Green 1995, Lanner 1996). Birds may also have some negative effects on forest regeneration in some situations, due to their predation of seeds.

This evidence indicates that there are strong ecological and economic reasons for sustaining healthy bird populations. If the value of $1,820 (U.S. dollars) is remotely accurate, then the pro bono contribution of birds to the boreal forest is in the millions of U.S. dollars per year. This value does not include other ecosystem services that birds perform, the increased value of the trees from higher growth rates, or other economic values such as the recreational and aesthetic value of birds.

Another viewpoint is the essential role that a healthy, forested ecosystem has in maintaining healthy forest bird populations. For example, forest land management is focused on sustaining forest ecosystems, of which birds are but one component. Even though we cannot yet identify all of the necessary components and links within the forest ecosystem, we have to rely on indirect measures of ecosystem health. One measure is the status of bird populations. Birds integrate many structural and functional aspects of the forest ecosystem, so understanding bird

populations is a link to understanding forest ecosystems. This is also one reason that birds have often been suggested as indicators or monitors of healthy forest ecosystems (Furness and Greenwood 1993).

Status of programs on sustaining boreal bird populations

Broadly varied publications have addressed the issues of sustainable use of forest systems and of sustaining wildlife populations. For example, in Minnesota, a Generic Environmental Impact Statement (GEIS) on timber harvesting and forest management was conducted to address concerns about the increased logging of trees (Jaakko Poyry 1992). Minnesota has continued with this effort by funding a long–term program called the Minnesota Forest Bird Diversity Initiative. The program is now in its eighth year of a 12–yr effort to monitor forest bird populations, to conduct selected research, and to provide education to managers and the lay public on issues related to the sustainability of forest bird populations (Green 1995). In the western Great Lakes region, Howe et al. (1997) reported that habitat management is a first step toward bird conservation, but indicated that species interactions and biogeographic factors can quickly complicate simple management prescriptions.

There have been several Canadian initiatives to provide a framework for bird conservation. Partners In Flight–Canada (1996) developed a "Framework for Landbird Conservation in Canada," which outlines the components of a coordinated land bird conservation program and includes monitoring, research, and applied conservation. On a smaller scale, the Federation of Ontario Naturalists, in conjunction with the Canadian Wildlife Service and others, described a framework for achieving land bird conservation that includes identifying priority species and habitats at multiple scales, developing habitat–based strategies to conserve birds, with identification of core area networks, and developed a monitoring strategy based on current monitoring, research, and inventory (Chesky 1995). Key to both of these plans are substantial investments in monitoring and research.

In northern Europe, many national programs and sets of management instructions have been developed for forestry to increase multiple–use and preservation of biodiversity in managed forests. National forest laws launched recently in many countries have placed a high priority on preserving biological sustainability, populations of less abundant species, special habitat types, and the total biodiversity of forested ecosystems. An important issue is that conservation should not be restricted to forest reserves (which are of crucial importance for some species), but managed forests are important to preservation of the overall diversity of communities and ecological processes at different scales (Tucker and Heath 1994).

The Wild Birds Directive of the European Union is another major vehicle for the conservation of ecosystems in northern Europe. For all species listed in the Bird Directive, every effort should be made to not decrease their population size or range due to human–related activities. The Nordic countries have the most responsibility for the conservation of boreal forest species within Europe. For example, in Finland there are 22 forest bird species included in the list of the Wild Birds Directive, and 14 of these are the responsibility of Finland, because >10% of their European population breeds in Finland (Rajasärkkä 1997).

DISCUSSION

Population variability

With the exception of economically important game mammals, birds probably have been studied more intensively than any other group of organisms. Long–term monitoring schemes such as the North American Breeding Bird Survey (Robbins et al. 1986), British Common Bird Census (Furness and Greenwood 1993), and Finnish land bird monitoring scheme (Koskimies and Väisänen 1991), provide comprehensive, ongoing databases covering several decades. Many other local studies provide databases covering 10 or more years

(Hogstad 1993, Welsh 1995, Howe et al. 1997).

A better understanding of the ecological factors that contribute to variability in boreal bird populations is critical, if society is to sustain populations over a variety of temporal and spatial scales. Holmes (1990) and other ecologists (e.g., Blake et al. 1992) argue that various factors influence variability in bird numbers, including: (1) successional changes in habitat structure; (2) variations in food abundance; (3) interactions with competitors and predators; and (4) events on wintering grounds. Local disturbances such as logging inevitably modify the character of these factors, thereby affecting population sizes. How these disturbances affect variability is unknown, but local populations of species that are adapted to disturbed habitats are likely to vary inversely with populations of late–successional species.

Every long–term study has reported that bird abundance varies considerably. Patterns of variation are typically complex and individualistic; as a result, information from a few local studies is difficult to apply to larger geographic scales (Taper et al. 1995). Conversely, large– scale and long–term trends are not always evident at local scales. Even for globally declining species, areas of population decline might be interspersed with areas of little change or even local population increase (Villard and Maurer 1996). An understanding of factors responsible for population variability, therefore, is an important and meaningful challenge (Mönkkönen and Aspi 1998).

Observed patterns of variability in bird numbers are consistent with a view that bird population dynamics operate on large spatial and temporal scales. Unlike many other groups of organisms (e.g., Thomas 1995), birds are able to recover from local perturbations such as defoliation by insects (Bell and Whitmore 1997) and logging (Virkkala 1987), as long as adequate source populations are maintained nearby (Pullman 1988). On the other hand, the negative effects of habitat degradation might take many years to be manifest. Site tenacity and survival of local adult birds may delay the effects of changes in habitat suitability (Bengtsson et al. 1997).

Even though population dynamics of birds appear to operate at large scales, local variability in bird abundance is of great interest because land management activities and conservation efforts typically occur at local (<1 km^2) scales. In addition, little is known about dispersal in bird populations. Generalizations about local variability in bird abundances are also confounded by sampling effects. Helle and Mönkkönen (1986) found a strong correlation between population variability and average population density in boreal forests of Finland; rare species showed greater variability in numbers. Part of this variation undoubtedly can be attributed to sampling errors and spatial variability within populations (Mönkkönen and Aspi 1998). Haila et al. (1996) documented a high degree of year–to–year stochasticity in the locations of bird territories in heterogeneous boreal forests. They attributed stochastic variation in many species to an overabundance of suitable sites. Individuals consistently avoided certain habitats, but within the remaining habitats, territory locations were highly variable and difficult to predict. Gaston and McArdle (1994), Link et al. (1994), and Mönkkönen and Aspi (1998) discuss methods for removing the variance caused by incomplete sampling or spatial patchiness within bird populations. Unless these effects are taken into account, Mönkkönen and Aspi (1998) argue that we know far less about variability in bird populations than we think.

Measuring density variability is important because it has been suggested that populations occupying sink habitats show higher temporal variability than do source habitat populations (Howe et al. 1991, Beshkarev et al. 1994). The identification of source populations and habitat, if they exist, is critical for sustaining populations, because regional existence of species is dependent on successful reproduction from population sources (Pulliam 1988, Pulliam and Danielson 1991). In Northern Europe, Järvinen (1980) suggested that some high–latitude populations are largely dependent on surplus individuals produced farther south in population source areas. In North America, it has been suggested that conservation of northern breeding areas is critical to population sources and the continual supply of individuals to sink, temperate regions of the United States, where breeding habitats have been fragmented and reproductive success is low (Terborgh 1992, Robinson et al. 1995). The large–scale evidence for any of these patterns is minimal and speculative.

Ecological factors underlying sustainability: density dependence and independence

The idea that boreal bird populations are regulated by winter mortality, particularly of young individuals, is widely accepted for both resident (Lack 1964, Lahti et al. 1998) and migrant birds (Fretwell 1972, Bailley and Peach 1992, Sherry and Holmes 1996). This concept suggests that in the breeding season, density–dependent factors are not particularly important in regulating boreal forest bird populations, but successful reproduction in the breeding grounds is essential to replenish populations. Järvinen (1987) suggested that mortality during the breeding season was density independent, both in southern and northern boreal populations of the Pied Flycatcher (*Ficedula hypoleuca*) and the Redstart (*Phoenicurus phoenicurus*) in Finland, whereas winter mortality appeared to be density dependent. Sherry and Holmes (1996) further argue that many Neotropical–Nearctic migrant land birds are limited at least partly by their winter habitats, but not by their breeding habitat. It is likely that some degree of population limitation may occur during all seasons, and that these limitations vary each year.

Boreal bird populations are characterized by large temporal variability in density, which implies that density–independent factors are more important (Hanski and Tiainen 1988). However, inferring that density dependence causes low variability is not necessarily a tenable statement. If the environment is variable or density dependence is delayed, the temporal variation of populations may be high, regardless of the operation of density–dependent factors (Gaston and McArdle 1994). Empirical studies have shown that terrestrial vertebrates, and birds in particular, show much lower variability in mean abundance than do invertebrate taxa (Hanski 1990). Among birds, the change in variability with mean abundance is more pronounced in territorial than in nonterritorial species, so that at high densities, territorial species tend to vary less than nonterritorial species. These patterns have been interpreted in terms of strong density–dependent population regulation in birds (via territoriality). However, as discussed by Mönkkönen and Aspi (1998), sampling error alone may produce such patterns.

Järvinen (1979) showed that the variability of bird density increased with latitude in Europe, a pattern that persisted even if the variance in the census data was controlled (Mönkkönen and Aspi 1998). Järvinen (1979) concluded that this pattern is a result of environmental (climatic) unpredictability increasing from south to north. Large temporal variability in population densities implies an increased probability of extinction (i.e., reduced sustainablity), but at large spatial scales, the relationship between variability and sustainability may not be strong. It is notable that Noon et al. (1985) found little support for a northward increase in variability in North American bird communities. A possible explanation for this discrepancy is the different latitudinal range between studies. In North America, most studies are from the southern edge of the boreal region, whereas in Northern Europe, many studies extend throughout the boreal region. For example, Järvinen (1979) specifically contrasted data from the southern temperate zone with those from the boreal in Europe. Few data in Noon et al. (1985) originated from the boreal zone. Also, Mönkkönen and Aspi (1998) suggested that density variability is particularly high in the north, but relatively low or constant among sub–boreal bird communities.

As shown by Hagan et al. (1996), these relationships may shift temporally as a result of habitat change. The density of forest–dwelling species may increase in some forest stands soon after the onset of logging in the surrounding landscape. The increased density can lead to lowered pairing and breeding success in bird populations, and thus to an inverse relationship between density and productivity (Hagan et al. 1996). Schmiegelow et al. (1997) found similar crowding in a large–scale experimental study in a boreal mixed forest in northern Alberta.

In summary, some evidence suggests that populations of boreal bird species are not generally limited by density–dependent factors, but populations are highly variable. Unfortunately, there is little information, except for a few species such as grouse (e.g., Newton 1994), on the relative contribution of factors that control populations. We do not understand enough about populations of boreal bird species to make predictions about how they are regulated. Furthermore, we know little about the relationship between population density and productivity. For instance, does high population density translate into high or low nesting success or production in the next generation? In one of the few studies available in the boreal forest, Mather and Welsh (1996) showed

a positive relationship between abundance and breeding evidence for 14 of the 27 boreal passerine species examined. The remaining 13 species showed no relationship between abundance and breeding evidence.

Population trends

In a relatively well−studied boreal area, Finland, more bird species have increased in abundance than have decreased with the conversion of more natural forest landscapes into intensively managed ones. The general trend from the past to the present has been for many of the common species to become more numerous, while many of the rarer species have declined. Populations of species with high affinities to old forests, such as the Siberian Jay (*Perisoreus infaustus*), Siberian Tit (*Parus cinctus*), and Three−toed Woodpecker (*Picoides tridactylus*), have decreased dramatically during the latter half of the 20th century, as a consequence of forest habitat loss and fragmentation due to intensive forestry (Helle 1985, Virkkala 1991). Although these patterns are well described, we do not know the precise mechanisms for these population declines. Among the few studied cases, Virkkala (1990) showed that in more pristine forests, Siberian Tit breeding success and the number of fledglings per nest were higher than in heavily managed stands. This was possibly associated with the lower abundance of invertebrates in managed stands than in natural stands (Petterson et al. 1995). However, the populations of Siberian Tits had declined more than expected by the loss of their preferred habitat, mature conifer forest. This suggests that other factors such as forest fragmentation, the deterioration in habitat quality, the selective removal of old trees, or climate change coupled with habitat changes are also involved in the population declines. In northern Finland, regional population changes (both decreases and increases) are more consistent than changes at the scale of individual forest remnants (Väisänen et al. 1986). For example, Virkkala (1991) also found that population declines of birds in managed forests of northern Finland were not simultaneously observed in virgin forest remnants. Capercaillie (*Tetrao urogallus*), Three−toed Woodpecker, Siberian Tit, Siberian Jay, and Pine Grosbeak (*Pinicola enucleator*), all of which have declined in northern Finland, have remained relatively stable in large blocks of virgin forest. In contrast, Helle (1986) found that populations of many bird species varied similarly in virgin forest and nearby managed forests.

In Canada, there are approximately 70 Breeding Bird Survey routes that fall within the *boreal forest*. We examined 30−yr trends (1966−1996) using these Breeding Bird Survey routes, which are available on a web site (Sauer et al. 1997). Of 62 species examined, there were insufficient data to examine trends for 11 species, seven species had significant ($P < 0.05$) trends (five negative and two positive), and the remaining 44 species had no significant trends. Species with negative trends included Chestnut−sided Warbler (*Dendroica pensylvanica*), Yellow Warbler (*Dendroica petechia*), Common Yellowthroat (*Geothlypis trichas*), Yellow−bellied Sapsucker (*Sphyrapicus varius*), and Least Flycatcher (*Empidonax minimus*). The Forest Bird Monitoring Program (Welsh 1995) has approximately 80 sites in the boreal forest of Ontario with three or more years of data for the calculation of trends in the 1987−1997 time period. Trends were estimated for 54 species (occurring in at least 15 sites). Eight species had significant ($P < 0.01$) trends, in which five were positive and three were negative. Species with negative trends included Eastern Wood−Pewee (*Contopus pertinax*), Winter Wren (*Troglodytes aedon*), and Golden−crowned Kinglet (*Regulus satrapa*) (Heather Dewar, Canadian Wildlife Service, *personal communication*). Long−term monitoring of birds in boreal Canada has not been completed on a scale that enables us to assess the status of populations. This is a serious impediment to our ability to assess the sustainability of boreal bird populations in North America.

Continent−wide−scale disturbances in boreal forests

Long−term, large−scale changes resulting from climatic instability during the Pleistocene have impacted the ranges of bird species and the composition of regional and continental species assemblages. The Quaternary paleoenvironmental fluctuations have been more drastic in the western Palaearctic than in the Nearctic region. European forests were greatly diminished in extent, persisting as altitudinal belts on southern mountains that were fragmented, isolated from each other, and became floristically depauperate (Huntley 1993). Continuous forest did persist, however, in eastern and central Siberia and China (Kurtén 1972). In North America, temperate

forests were able to better maintain taxonomic diversity and a more extensive and continuous presence (Webb 1988). Moreover, temperate forest zones of North America remained in close contact with the tropics during the glaciations (e.g., CLIMAP 1976), enabling a continuous interchange of tropical and temperate avifaunas. The Saharan desert was, by contrast, more extensive during the glacial stages (CLIMAP 1976). As a result, forest−associated fauna of eastern North America, including those that use the boreal forest, probably had better opportunities of finding refugia than did those of Europe. Huntley (1993) attributes the low taxonomic diversity in European forests principally to the limited area available to forest taxa. The Quaternary paleoenvironmental conditions have obviously affected ecological attributes of extant species (e.g., behavioral plasticity, habitat preferences, etc.) and, consequently, have had an influence on how species respond to contemporary, human−induced landscape changes (Mönkkönen and Welsh 1994). These large−scale changes have been implicated as critical events in the speciation of many North American species, such as the New World warblers (Mayr 1946, Bermingham et al. 1992). However, recent evidence using mitochondrial DNA questions the importance of Late Pleistocene glaciation events in the speciation process (Klicka and Zink 1997). Regardless of the specific timing of speciation, many boreal species have been exposed to a variety of disturbances, which may have predisposed them to be relatively plastic to habitat and environmental changes.

Landscape−scale disturbances in boreal forests

Disturbances such as forest fires, insect outbreaks, and large−scale wind and ice storms affect the structure of forest landscapes and forest stands at intermediate scales. This has resulted in heterogeneous landscapes with a wide variety of different successional stages of forests at any given time (Haila 1994). These disturbances occur in the time scale of decades to a millennium, and may extend from hectares to millions of hectares in area. Secondary forest succession, initiated by a natural or human−caused catastrophe, is a directional change in communities from a pioneer stage (more or less open ground) to a climax stage. The process lasts from one to several hundred years in the boreal setting (Heinselman 1996), and it is a useful framework for studying and understanding natural dynamics of the boreal forest.

Landscape−level effects on birds have recently become better documented (Helle and Järvinen 1986, Rolstad and Wegge 1987, Opdam 1991, Andren 1994, McGarigal and McComb 1995, Kurki et al. 1997), and indicate the effects of regional forest area, patch size, and isolation on the number of species or densities of species. The influence of landscape composition, configuration, and connectivity on population dynamics implies that the impact of forest change (due to human or other disturbances) on the status of populations cannot be extrapolated only from local measures of forest character and change. Early documentation of landscape−scale effects was predominantly for forest patches in agricultural landscapes (Opdam 1991). Examples of studies in forested landscapes are becoming more common, and several recent studies have been conducted in a boreal forest context. For example, Rolstad and Wegge (1987) presented a graphical model to predict the response of Capercaillie males to fine−grained and coarse−grained forest landscape fragmentation. DesRochers and Hannon (1997) found that boreal forest songbirds were twice as likely to travel through 50 m of woodland than through 50 m in open habitats when attracted by recordings of chickadee mobbing calls. Kurki et al. (1997) linked landscape change with the increase of fox (*Vulpes vulpes*) populations and the subsequent reduced breeding success of grouse, particularly after peak vole years. Schmiegelow et al. (1997) studied the effect of fragmentation on the richness, diversity, turnover, and abundance of breeding bird communities in old boreal mixed forest. Richness of Neotropical migrants declined in both connected and isolated fragments, resident species declined in isolated fragments, and short−distance migrants, most of which are habitat generalists, did not change. However, Schmiegelow et al. (1997) concluded that the magnitude of the fragmentation effects was small compared with those observed elsewhere, possibly because the fragments were embedded in a matrix of uncut forest. If species have evolved where frequent disturbances create a naturally heterogeneous landscape, then they may better cope with human−induced landscape changes (Hansen et al. 1991, Hansson and Angelstam 1991, Rudnicky and Hunter 1993, Schmiegelow et al. 1997).

The surrounding landscape matrix around a forest stand has also been shown to influence the composition of breeding birds within a stand. For example, Pearson and Niemi (1998) found some breeding bird species to be

more common in less suitable habitat if this habitat was surrounded by favorable habitat. Similar patterns were summarized by Andren (1994) in the Palearctic. Likewise, Väisänen et al. (1986) showed that the breeding bird community of a forest stand changed along with changes in the surrounding landscape, although the forest stand itself remained unchanged.

Patch– or stand–scale disturbances in boreal forests

Small–scale patch dynamics maintain the heterogeneity and diversity of forest stands. Here, the spatial scale varies from gaps of individual trees to changes in entire stands. Small–scale patch dynamics (gap disturbance) have two important consequences for birds in boreal forests. First, they create openings in climax stands of forests, providing habitat for species that require young forests. In these cases, both forest–interior and early–successional species are able to coexist in natural landscapes, even without large–scale disturbances (Lent and Capen 1995). Small regeneration patches increase the amount of habitat edge in a given area without fragmenting the landscape. Second, patch dynamics often maintain a considerable deciduous component in climax coniferous forests (Syrjänen et al. 1994) because of the open canopy in many of these forests. Deciduous trees are important for boreal birds such as woodpeckers and tits, and for foraging by many small passerines. Consequently, bird density and diversity in boreal bird communities have often been found to correlate positively with the proportion of deciduous trees (Haapanen 1965). These patterns match well with the intermediate disturbance hypothesis (Connell 1978) that the greatest effective heterogeneity occurs in intermediately disturbed areas, where numerous species can coexist.

Stand age is one of the most important variables affecting bird species density and community structure in the boreal forest (Helle 1985). Compared to temperate regions, relatively few studies have assessed successional patterns in boreal forest bird communities (Helle and Mönkkönen 1990). There is considerable variation in the patterns of response by forest birds during succession. For instance, Helle and Mönkkönen (1990) and Helle and Niemi (1996) found that diversity of the breeding bird community generally increased with increasing stand age in both Eurasia and North America. However, a variety of studies contradict this general pattern (e.g., Morgan and Freedman 1986, Westworth and Telfer 1993, and Kirk et al. 1996). Little consensus has emerged on how bird densities vary with successional age.

Human impacts on boreal forests

Fennoscandian forest landscapes have been influenced for centuries by slash–and–burn cultivation and charcoal, tar, and timber production (Esseen et al. 1997), but in many areas, forest harvesting started only a few decades ago or even more recently (see Mönkkönen and Welsh 1994, Syränen et al. 1994). Based on this historical scenario, Mönkkönen and Welsh (1994) suggested that contemporary avifaunas are not likely to be equally affected by present human impacts. They distinguished three species groups in the Holarctic forest bird fauna according to their "sensitivity" to human impact, varying from less sensitive "European" fauna to particularly sensitive Nearctic species. Boreal species of Siberian–Canadian origin were supposedly of intermediate sensitivity.

Modern human land use affects boreal ecosystems and their bird communities in many ways. In the boreal zone, forestry plays the main role and has replaced forest fire as the dominant disturbance (Brumelis and Carleton 1988), but there is considerable variation in forestry practices throughout the boreal forest. Use of timber and other forest products has had a long tradition in northwestern Europe, especially since World War II (Mönkkönen and Welsh 1994). Because of the long history of forest exploitation in the Nordic countries, little if any old–growth forest still exists. Old forests in natural condition are almost completely restricted to protected areas, and they compose <5% of all forest area in Fennoscandia. In northern Russia and especially in Siberia, on the other hand, the impact of forestry has been limited thus far, but this is rapidly changing (Myers 1997).

In North America, logging is a relatively recent activity; in most areas of the boreal forest, it also has occurred

primarily after World War II, except in the eastern, southern, and western fringes. Records for the acreage of old–growth forests in the North American boreal forest are relatively poor, because most areas were burned at relatively frequent intervals and the percentage of the landscape with pure stands of old trees (e.g., > 100 yr old) was probably always relatively small. In most areas, the number of super–canopy, fire–resistant trees like white pine (*Pinus strobus*), and the acreage of old–growth lowland coniferous forest such as black spruce (*Picea mariana*), tamarack (*Larix laricina*), and white cedar (*Thuja occidentalis*), were probably greater prior to logging activity.

In considering forest fragmentation, one geographical pattern needs emphasis. Temperate deciduous forest landscapes south of the boreal are mainly fragmented by agriculture, roads, power lines, and urban development, resulting in permanent habitat loss for forest organisms. Boreal forest landscapes are influenced mainly by forest harvesting, with less permanent habitat loss. Much of our knowledge on fragmentation effects is based on studies performed in temperate areas; hence, the results cannot be directly applied to boreal settings (Huhta et al. 1996, Gustafsson and Hansson 1997).

To some extent, regeneration of forests after clear–cutting and after natural disturbance is similar. Likewise, commercial thinning of forests and gap disturbance may provide similar habitats for birds. These similarities, however, are superficial. Forest fire has been the dominant regeneration force in the boreal region, and there is a profound difference between natural and logged–habitat disturbances. For example, fire intervals are highly variable and may range from 20 or 30 years to >100 years (e.g., Heinselman 1973, 1996, Zackrisson 1977, Bradshaw 1993, Ward and Tithecott 1993), whereas logging rotations occur at more regular and shorter intervals. Dry sites generally burn more frequently than moist sites, and some moist refugia may have escaped forest fire for hundreds of years or longer. One of the main differences between natural and logged stands (irrespective of their age) is the amount of dead and damaged trees remaining on the site (Niemi and Probst 1990). This difference affects many aspects of these stands, such as the abundance of hole–nesting species and species that feed on invertebrates living in such trees (Esseen et al. 1997, Schulte and Niemi 1998). In Fennoscandia, fire elimination leads to spruce *(Picea)* dominance in previously mixed stands of pine (*Pinus*), aspen (*Populus*), and birch (*Betula*), and hence, a reduction in the presence of mixed or deciduous–dominated forests. Several bird species that are particularly affected include woodpeckers and the Long–tailed Tit (*Aegithalos caudatus*) (Angelstam and Mikusinski 1994).

In moist sites, the ground is often plowed after clear–cutting, which also alters natural patterns of succession. In northern Europe, silvicultural rotations are often shorter than in natural forests, so older stands are often rare in intensively managed forest landscapes (Esseen et al. 1997). In contrast, the average age of forest stands in Ontario is getting older because logging rotations are less than the rate of forest fire. In many cases, only the well–stocked or prime stands are logged, so the older, less productive stands are left. Forest fires do not discriminate between prime or unproductive stands; hence, the managed landscape mosaic is considerably different from the landscape pattern created by fire (D. Welsh, *personal communication*).

There are many additional ways in which humans have influenced characteristics of the boreal forest, each of which has direct, but different, effects on bird populations. Logging, particularly the associated policy and legislation of cutting, has dramatically reduced the range of patch sizes in the boreal forest. Most cuts tend to be smaller than the average burn size. Most burned areas are hundreds to thousands of hectares in extent (Zackrisson 1977, Heinselman 1996), whereas logging tends to be in the tens, or occasionally in the hundreds, of hectares. In addition, logged areas have many roads that provide access to the forests (Esseen et al. 1997). Hence, the impact of forest management is alteration of the spatial and temporal pattern of the boreal forest into a fine–grained mosaic of relatively small patches with the high quality timber removed, interconnected with roads, and patches of lower quality timber left in the landscape.

Fire suppression has also had major, but largely unknown, effects on the boreal forest. Fire suppression allows a build–up of fuel in boreal systems that greatly increases the risk, severity, and inability to control a forest fire. In addition, there is an interaction between fire and outbreaks of spruce budworm. Such outbreaks have increased in size and duration in recent history, probably due to harvesting practices and fire suppression (Blais 1983). Moreover, fire control is expensive. In Ontario, from 1990–1994, annual expenditure on fire suppression was

approximately $27 million in Canadian dollars (Canadian Council of Forest Ministers 1997).

In contrast to the concerns about the limited proportion of old–growth forest in the landscape due to logging, most often the management of young stands for the benefit of wildlife is neglected. A major emphasis in reducing rotation time in conifer stands of the boreal forest is to truncate the early stages and completely eliminate mixed–deciduous and shrub stages. Conifer stands are often planted, and then chemical and mechanical controls are used to eliminate deciduous competitors. Another concern is the conversion of forests to other forest types. For example, some pure coniferous forest types in Ontario are being converted to mixed coniferous–deciduous forests as a result of management practices (Hearnden et al. 1992). Yet, in northern Europe, the reduction of deciduous trees in intensively managed coniferous forests is implicated in the decline of some woodpecker species and secondary cavity–nesting species (Angelstam 1992). Even though the quantitative evidence on the effect of some of these management practices is poorly understood, the empirical knowledge available for most bird species is satisfactory to predict the consequences for many of these practices.

In Fennoscandia, there have also been tremendous changes in many mesic and moist forest sites, due to ditching and reductions in the deciduous shrub and tree component of forests (Esseen et al. 1997.) In North America, ditching of moist forests and active management of deciduous components in coniferous forests have been limited, except in plantations (in the case of the latter).

Consequences of not managing for sustainability of bird populations

Managing for sustainable bird populations inevitably involves a cost in terms of direct expenses or appropriated resources. In the most extreme case, a single territorial pair of Northern Spotted Owls might require >3000 ha of old–growth forest, which is valued at >$1 million (U.S. dollars) if sold in today's market. Few species demand such large areas and specific habitat conditions. Nevertheless, species that are most likely to be threatened in boreal forests are those requiring relatively undisturbed conditions (Järvinen and Väisänen 1978, Edenius and Elmberg 1996, Kirk et al. 1996). Habitat protection for these species requires maintenance of forest reserves, where logging is prohibited or at least permitted only at low levels. This raises the question of "how much area is enough to protect and sustain these populations?" The answers to this question are complex, because extensive areas of virgin forest still remain, providing sources of immigrants for disturbed forests.

In addition to the exclusion of certain lands from silviculture, managing for sustainable bird populations involves other measures that may reduce yields in managed forests. Cavity nesters like woodpeckers and nuthatches require old or diseased trees that have little economic value (Angelstam and Mikusinski 1994). There is a wide variety of guidelines on the number of dead and live trees to leave in harvested areas (Hunter 1990), yet no experimental studies have quantified the positive effect that these trees have on birds.

Control of insect pests such as spruce budworm and gypsy moth (*Lymantria dispar*) reduces the food available to bird populations (Bell and Whitmore 1997). Species such as Bay–breasted (*Dendroica castanea*) and Cape May Warblers (*Dendroica tigrina*) that specialize on insect outbreaks (Holling 1988) are particularly vulnerable to large–scale insect control programs. Economic loss of harvestable trees to insects represents another potential cost of the sustainable management of bird populations, although the net effect is not well documented. Another concern is the availability of habitat during endemic years. For example, during low endemic years of spruce budworm cycles, the Cape May Warbler is found uncommonly in large white spruce (*Picea glauca*), but these trees are prime targets for logging. Little is known about the importance of these trees to budworm specialists like the Cape May Warbler during these low endemic periods.

Birds are also important seed dispersers of economically important trees and shrubs. Lanner (1996) has eloquently described the symbiotic relationship between many pine species and corvids, with examples from around the world, especially in boreal systems. The pine and corvid symbiosis, the coexistence of a plant and animal in a mutually beneficial partnership, allows for substantial dispersal of pine seeds far from the maternal tree. Although the number of bird–dispersed plants in boreal forests may be low compared with plants in tropical

ecosystems (Pastor et al. 1996), many species that breed in northern forests are also important seed dispersers during migration. Thompson and Willson (1979) noted that the fruiting of plant species in Illinois reaches a peak during the period of peak spring migration of songbirds. Important fruit dispersers include the many species of thrushes and several warblers that breed in boreal forest regions. Undoubtedly, many plant species in both the Nearctic and Palearctic benefit by the movements of birds.

Birds are the primary objects of extensive and economically significant recreational activities. Currently, tens of millions of Americans spend more than $20 billion (U.S. dollars) annually on bird feeding, travel, and bird–watching equipment (Kerlinger 1993). During 1991, for example, more than 24 million U.S. citizens took trips for the expressed purpose of watching wild birds. By comparison, 14 million took trips for hunting and 35 million for fishing (U.S. Forest Service 1995). Although only a fraction of these visits centered on boreal forests, many of the species valued by bird–watchers breed in boreal forest regions and migrate to more populated parts of North America during nonbreeding seasons. Economic losses of logging revenues also must be balanced against the potential for future recreation in remote boreal forest regions. According to the U.S. Forest Service (1995), the three fastest growing recreational activities in the United States are hiking, backpacking, and primitive–site camping.

Knowledge gaps on boreal birds

Life histories of species can differ among geographical locations and, thus, suites of species from distinct biomes may respond in unique ways to landscape change (Hansen and Urban 1992, Mönkkönen 1994, Mönkkönen and Welsh 1994). It is difficult to generalize across biomes about the effects, for example, of habitat fragmentation. If an organism–centered view is adopted, generalizations about species within a biome are problematic because species' life histories differ. Hence, there is no substitute for specific knowledge about the life history and ecology of a species in a regional species pool.

We still lack a thorough understanding about the effects of habitat loss and fragmentation on populations at the landscape level and how to remedy their negative impact (Howe et al. 1997). These are among the primary concerns of conservation biologists. Species–centered management, however, is doomed to be too complicated and controversial and, therefore, we must focus on ecosystem management and preservation of processes that are critical for assemblages of ecologically similar species (Pastor et al. 1996, Niemi et al. 1997).

There is considerable geographical variation in the amount of existing information on boreal birds. Boreal avifaunas are relatively well known for some areas in North America and in northwestern Europe, whereas little information exists for large areas in boreal Canada and Siberia. Similarly, we need to know more about natural disturbance regimes for different regions of the boreal forest and their effects on bird communities. Disturbance regimes certainly differ among geographical locations, along with climatic, topographic, and ecological conditions.

Neutral landscape modeling has identified critical thresholds in landscape composition, which define quantitatively the point at which the landscape becomes fragmented (Gardner et al. 1987, With 1997). Critical thresholds imply that the effects of fragmentation on connectivity and, ultimately, on population persistence, are nonlinear (Gardner et al. 1987, Andrén 1994). Loss of species with increasing degrees of fragmentation and habitat loss is subtle in the beginning, but after some threshold in proportion to original habitat, the decline in diversity may be very rapid. Andrén (1994) reviewed the existing literature on mammals and birds in habitat patches in landscapes with different percentages of suitable habitat. He concluded that critical threshold levels for these taxa are between 10% and 30% of suitable habitat in the landscape. Below this level of available habitat, the species population will decline faster than expected from habitat loss alone. Whether or not this empirical critical threshold also implies the point at which the risk of population extinction increases is not known. This should not be interpreted to mean that 10–30% of the original habitat area is enough for boreal forest species (Edenius and Sjöberg 1997, Mönkkönen and Reunanen 1998). Moreover, most of these models have been developed for the agricultural/forest interface, with total loss of forest due to habitat conversion. In the boreal

forest that is fragmented by logging activity or other disturbances, the forested habitat is altered, but most often is not converted to another use.

Comparisons of Old and New World bird species indicate that Nearctic species may show a higher degree of habitat specialization than Palearctic species (Mönkkönen 1994). This pattern also seems to apply to the use of foraging substrates. If boreal birds tend to be habitat generalists in the Palearctic region, then these differences imply that sustainability of boreal bird populations may be more difficult to achieve in the Nearctic than in the Palearctic. In addition, more intense management of Nearctic boreal forests into Fennoscandian–type commercial forests (e.g., reductions in shrub layers or reductions in tree diversity) will probably have even more pronounced impacts on bird species than what has been observed in Fennoscandia.

Tools for management of sustainable boreal bird populations

Proper management for ecological sustainability incorporates disturbance as a natural part of the managed ecosystem (Urban et al. 1987). Present silvicultural practices have rescaled patterns of disturbance in time and space. Ecologically sustainable management incorporates the concept that forest logging be matched with natural disturbance regimes. This would ensure that, at the landscape or regional scale, there is some mixture of disturbed, recovering, and mature or old–growth forest. This would provide habitat not only for species requiring mature or old–growth forest, but also for species dependent on disturbed areas and ecotones.

Today's revolution in information technology provides numerous tools that can be used to promote sustainable management of bird populations. Remote sensing with satellite imagery increasingly is being used to refine our understanding of bird–habitat relationships (O'Connor et al. 1996). Although traditional ecological studies have been restricted to stand–level attributes, satellite images introduce new landscape–level variables such as patch geometry, proportion of different habitat types within a given radius, distance to important land features, and landscape heterogeneity (Grenier et al. 1994, Chou and Soret 1996, Mladenoff et al. 1997). Most studies involving computerized satellite images employ geographic information systems (GIS) to calculate landscape variables. GIS data, togetherwith large–scale bioclimatic variables, allow researchers to develop predictive models of species' distributions over broad areas where censuses are unavailable (Aspinall and Veitch 1993, Venier et al. 1998). As satellite images and GIS are applied more widely, they will continue to improve the ability of resource managers to predict outcomes of land use strategies. However, various questions remain on the accuracy and scale of applications that are possible with remote–sensing technology for making predictions about boreal bird distributions, especially in light of the high variability for many of these populations.

To consider a wide range of land use options and mostly unknown consequences, resource managers today have embraced the concept of adaptive management (Holling 1978, Walters 1986), a dynamic decision–making strategy that is continuously refined as information accumulates from experience. Although adaptive management is widely established as an ideal (Kessler et al. 1992), applications have rarely met the objectives envisioned by proponents. Problems have arisen because information has been incorporated from a narrow range of sources, and management alternatives have relied too heavily on linear–systems models (McLain and Lee 1996). Recent developments in computer–based artificial intelligence have led to *decision support systems* that can apply large bodies of information to resource management problems (Loh et al. 1991, Linehan 1994). Most published decision support systems for forest management have been aimed at economic harvest strategies, with little or no consideration of biodiversity conservation (Thompson and Weetman 1995). Recently, multiple–use planning methods have been vigorously developed in the Nordic countries, especially numerical optimization procedures and choice models for decision making (Kangas and Kristiansen 1995). These methods have not yet gained general approval in forestry practice, and decisions are still mainly based on descriptive approaches. Sustainable management of wildlife populations can be incorporated into decision support systems (Kangas et al. 1993), although effective consideration of many species simultaneously presents an enormous challenge (Davis and Martell 1993, Burkman et al. 1994).

Simple decision support systems lead to single decisions based on a fixed set of existing conditions. Possingham

(1997) calls these static decision−making tools, because the optimal strategy does not take into account past decisions and expected consequences of the current decision. He introduces a more complex, dynamic decision support system based on Markov decision theory. This approach is useful for situations in which decisions need to be made continuously. In such cases, the optimal strategy depends on the current state of the system, and it changes as the system moves from state to state. Unfortunately, dynamic decision−making strategies require enormous computational effort for complex problems, and Possingham's method does not lend itself to situations in which the number of states that a system can occupy is large. Nevertheless, sustainable management of bird populations in boreal forests will require decision−making tools of this kind if human activities continue to alter extensive wilderness regions and natural disturbance regimes. A landscape−scale model (Mladenoff et al. 1996, He et al. 1998, He and Mladenoff 1999) of this sort is currently being linked with a variety of bird information, including habitat relationships, landscape context, and life history, for forests in Minnesota and Wisconsin, United States.

CONCLUSIONS

Questions outnumber answers in our analysis of sustainability of bird populations of boreal regions. Current knowledge identifies an important role for birds in boreal forests, provides guidance for future research, and reveals issues that should be approached with caution. These issues include (1) our ability to mimic natural disturbance regimes with management; (2) predicting the effects of forest fragmentation on boreal bird species; and (3) understanding the relationship between bird population density and productivity. Management decisions ultimately are made in a local or regional context, and are always constrained by economic and political forces. The essential role that research on birds can provide is to clarify important ecological concerns and variables that not only will help to sustain bird populations, but also will contribute to the long−term health of the boreal forest for all species, including humans.

RESPONSES TO THIS ARTICLE

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ACKNOWLEDGMENTS:

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