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Three decades of avian research on the Bartlett Experimental Forest, New Hampshire, U.S.A.

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A B S T R A C T

Ornithological research from the Bartlett Experimental Forest in New Hampshire, U.S.A. has provided information useful for developing management practices for northern hardwoods forests and understanding factors affecting avian populations. This work also serves to illustrate numerous features and characteristics of experimental forests that facilitate research. One example is opportunities for long-term and interdisciplinary research, illustrated by the application of a 25-year data set on snag longevity collected as part of a silvicultural experiment to evaluate habitat conditions for cavity nesting birds. Experimental forests also provide a conduit for information to managers by virtue of their collocation with U.S National Forests (Stoleson and King, this issue). At the time bird research was initiated on the Bartlett Experimental Forest the potential for forest management to fragment habitat in forested landscapes in the northeast U.S.A. was unknown, because the only studies on this topic were from the Midwest or Mid-Atlantic States where forest patches are isolated by agricultural or suburban development. Research on the Bartlett Experimental Forest has provided managers with region-specific information on the potential for silviculture and associated development to fragment forests, indicating that unlike less forested landscapes, cowbirds (*Molothrus ater*) are rare, and that edges created by forest roads in extensively forested landscapes have little effect on mature forest birds. Research from the Bartlett Experimental Forest has also provided guidance to managers for providing habitat for shrubland birds, both in terms of silvicultural prescriptions (Yamasaki et al., in preparation) and patch area (Costello et al., 2000). Experimental Forests also provide access to facilities and infrastructure, such as road networks, laboratory space and housing, to facilitate research requiring frequent access to sites, such as radio telemetry investigations (King et al., 2006; Chandler, 2006).

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1. Introduction

Bird populations face global conservation challenges, with 1 in 8 species facing a high risk of extinction in the near future according to a recent IUCN report (IUCN, 2009). Birds are highly valued by the American public. A recent US Fish and Wildlife Service analysis concluded that 20 percent of the US population are interested in bird watching, contributing approximately 85 billion dollars to the economy and creating over 800,000 jobs (La Rouche, 2001). Birds also perform significant ecosystem services with consequences for human health and well being, including pest control, sanitation, seed dispersal and pollination (Sekercioglu et al., 2004). Birds are considered indicators of ecosystem health, and thus their status can indicate the status of other species. For these reasons, conservation research on birds represents an area of exceptional interest to scientists and professionals. Experimental Forests are dedicated to long-term research, and provide access to a wide diversity of study areas, infrastructure, opportunities for controlled manipulations, and integration with other types of long-term data (Lugo et al., 2006; Adams et al., 2008). These features have facilitated important advances in a number of areas of avian research at the Bartlett Experimental Forest, including research on the effects of forest management, responses to disturbance, and other aspects of avian ecology and conservation. The research team includes wildlife biologists and foresters who work together to design treatments to address questions regarding the effects of silviculture on woody vegetation, birds, and other vertebrate taxa.

1.1. The Bartlett Experimental Forest

The Bartlett Experimental Forest is located within the Saco Ranger District of the White Mountain National Forest (WMNF),

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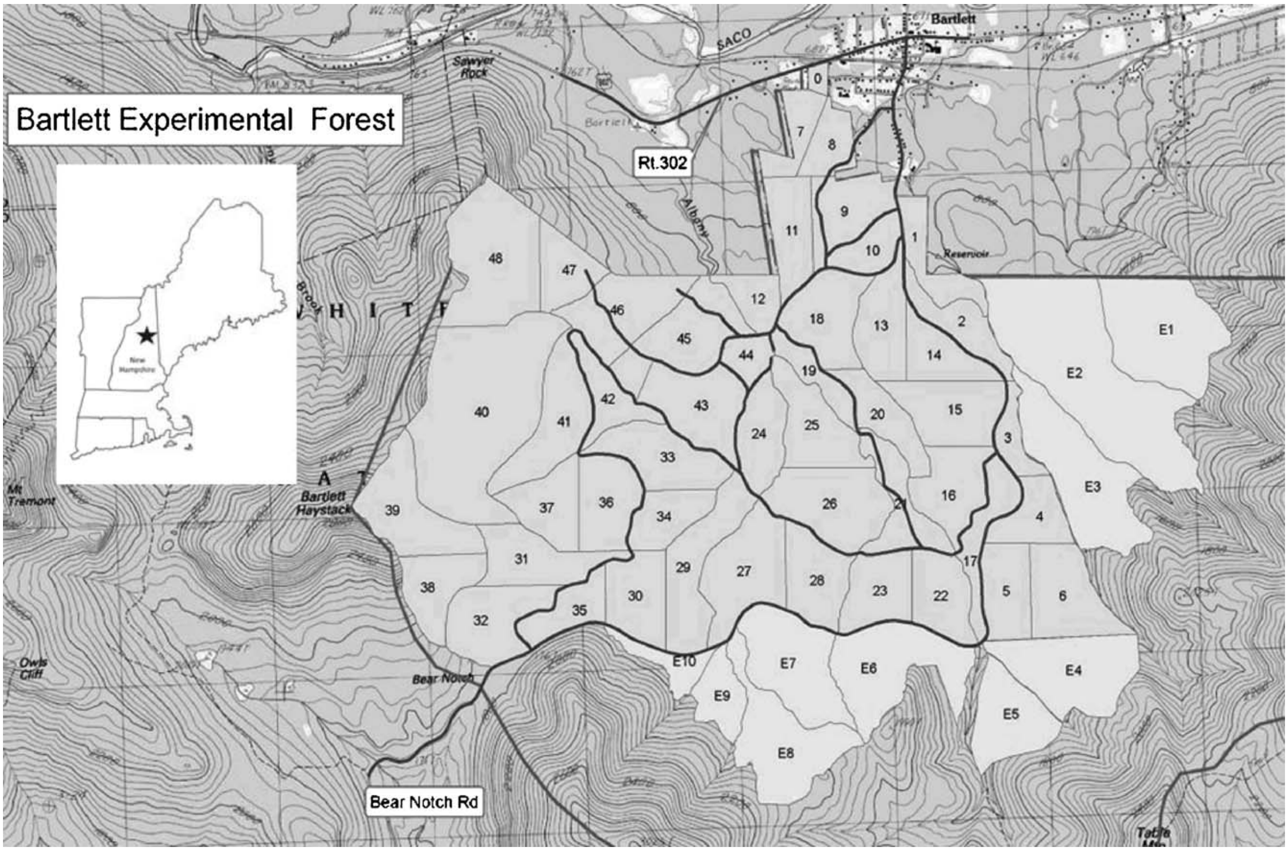

Fig. 1. The Bartlett Experimental Forest, Bartlett, New Hampshire, U.S.A. The numbered management units within the original extent of the Bartlett Experimental Forest is shown in medium gray, and the portion added as part of the 2005 White Mountain National Forest Land and Resource Management Plan is shown in light gray. The inset shows the location of the Bartlett Experimental Forest with the state of New Hampshire and in relation to the surrounding northeastern states.

which is part of the National Forest system, in the state of New Hampshire in the northeastern U.S.A. (44°04′N, 71°17′W; Fig. 1). The Bartlett Experimental Forest is managed by the Northern Research Station, which is part of US Forest Service Research and Development. Research activities began at the Experimental Forest when it was established in 1931. Originally 1,052 ha, its size more than doubled to 2,343 ha with the signing of the 2005 WMNF Land and Resource Management Plan. Elevations range from 207 m in the Saco River valley to 976 m, with aspects primarily to the north. The Bartlett Experimental Forest represents conditions of soils, elevation, climate and tree species composition typical of many forested areas throughout New England and northern New York. In the late-19th century, the lower elevations were selectively logged and some portions cleared for pasture. Fires are infrequent, however, a hurricane in 1938 did widespread damage at higher elevations on the forest. An ice storm in 1998 was the most recent large-scale natural disturbance, impacting mostly higher elevation stands. Occasional wind storms are common disturbances, but of relatively small scale. Currently, the landscape surrounding the Bartlett Experimental Forest is 97% forested, with <10% of the forest <15 years old (U.S. Forest Service, 2005).

The climate in the Bartlett area includes warm summers during which daytime temperatures reach the low 30s°C and cold winters, with temperatures frequently as low as −5 °C and snow accumulation to depths of 150–180 cm (Adams et al., 2008). Average annual precipitation is 127 cm, distributed throughout the year. The soils at the Bartlett Experimental Forest are spodosols, developed on glacial till derived from granite and gneiss. The soils are moist but, for the most part, well drained. The black humus layer of the soil is nutritionally rich for plant growth, while lower mineral soil layers are nutritionally deficient. In many places the soil mantle is very shallow; boulders and rocks are common. The forest is dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*). The upper elevations support stands of red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*). Softwoods such as eastern hemlock (*Tsuga canadensis*), balsam fir, and spruce are commonly mixed with hardwoods, especially on cool steep slopes or on the poorly drained soils at lower elevations. Although white pine (*Pinus strobus*) occurs mostly in stands at lower elevations, scattered specimens can be found over a large part of the forest.

2. Interdisciplinary research on silviculture and birds

2.1. Bird use of snags and snag management

The Bartlett Experimental Forest has a rich history of 75 years of northern hardwood silvicultural research that has produced seminal works on topics including ecological site classification, regeneration, thinning, growth and yield, management options, old growth characteristics and natural succession (e.g., Leak et al., 1997; Solomon, 1977, Solomon and Frank, 1983; and others). The integration of bird research and silvicultural studies at the Bartlett Experimental Forest provides an excellent example of the opportunities for interdisciplinary research and access to long-term data that make work on Experimental Forests so productive.

Forest practices require the careful consideration of the effects of forestry on non-timber values, and work at the Bartlett Experimental Forest has made a substantial contribution to our understanding of the effects of silviculture on birds and other wildlife, as well as on how to integrate these values into forest management. Foresters and wildlife biologists recognize the importance of standing snags and coarse woody debris as interdependent habitat components within managed forests in New England (DeGraaf and Shigo, 1985; Tubbs et al., 1987). Both standing snags and coarse woody debris provide numerous foraging opportunities and cavity nesting and roosting sites for various woodpeckers (i.e., primary excavators) and secondary cavity-using birds while standing (Healy et al., 1989; Welsh et al., 1992; DeGraaf and Yamasaki, 2001). Bird use of snags varies with size and type of defect, and although foraging or nesting activity occurs in 90 percent of snags, excavated cavities are found in far fewer (6%) snags (Yamasaki and Leak, 2006).

This information on avian use of snags has been highly valuable for short-term planning; however, more recently it has become clear that long-term planning is required to assure snag recruitment throughout the life of the stand. Yamasaki and Leak (2006) addressed the issue of snag longevity on the Bartlett Experimental Forest, which represents an early effort at advancing coordination between foresters and the interests of forest bird communities while capitalizing on a 25-year long dataset on tree mortality. Foresters understand the importance and value of long-term growth studies with individually marked trees and repeated measurements (Solomon, 1977; Solomon and Frank, 1983; Leak et al., 1997). Following the mortality component in these types of studies can give habitat biologists and foresters further insights into the snag longevity patterns in other forest types in the region. Using data on snag longevity from a long-term hardwood growth study on the Bartlett Experimental Forest (Solomon, 1977), Yamasaki and Leak (2006) examined the fate of 568 snags and found that approximately one-third of the oldest dense hardwood sawtimber snags were still standing 20–25 years after death and 17% were still visible on the ground. Seventeen percent of the older moderately dense hardwood sawtimber snags were standing 15–20 years after death, 50% were still visible on the ground, and 33% had decomposed. Pole-sized snags appeared to stand for shorter times than sawtimber and large sawtimber snags. Percentage of decomposed poles increased steadily over time. These results have proven to be useful in predicting future wildlife habitat conditions in managed stands, as well as providing better rates of decomposition information when modeling coarse woody debris.

2.2. *The effect of silviculture on bird habitats and populations*

Forest management activities have come under increasing public scrutiny in recent years, especially on public lands, where managers need to state the effects of forest management practices on other resources, especially wildlife such as birds (DeGraaf and Chadwick, 1987). Long-term silvicultural research on tree regeneration methods on the Bartlett Experimental Forest has provided additional opportunities for interdisciplinary ornithological research by Yamasaki et al. (unpublished results), who compared bird communities in stands treated with clearcutting and shelterwood harvests. Clearcutting is a widely used silvicultural technique that has received particular public criticism, which has led managers to emphasize alternative forms of silviculture. The most likely silvicultural alternative in areas that are esthetically sensitive is low-density shelterwood cutting (Miller et al., 2006), which allows abundant sunlight to reach the forest floor but softens the visual impact. Low-density shelterwoods in northern hardwoods commonly leave a residual basal area of about 7–9 m^2/ha. For a conventional shelterwood the residual would consist of mature trees in preparation for a final removal a few years later. For a deferred shelterwood, the residual trees would be small sawtimber that would add volume and quality over the next few decades.

Partial cutting, such as single tree selection or the initial stage of a shelterwood cut, appear to have great potential for managing forest birds because it alters the vegetation structure in a stand enough to permit the establishment of at least some early-successional birds without eliminating all of the mature forest bird community (Webb et al., 1977; Annand and Thompson, 1997). King and DeGraaf (2000) reported that differences in bird species distribution among treatments were the result of differences in habitat structure among treatments. Bird species diversity and species richness were significantly higher in shelterwoods than either mature forest or clearcuts, although there were bird species that occurred exclusively, or nearly so, in each of the three treatments. Similarly, DeGraaf and Chadwick (1987) found that breeding birds could be grouped as either mature forest or early-successional stand condition obligates.

Experimental harvests on the Bartlett Experimental Forest provided the opportunity to compare the effects of a clearcut and a low-density deferred shelterwood (Fig. 2) on tree regeneration and songbird richness over an 8-year period following harvests on each (Yamasaki et al., unpublished results). A paired comparison of clearcut and shelterwood areas showed that clearcutting with no residual overstory provided a much higher proportion of early-successional tree species, and much lower proportion of beech and striped maple regeneration. Clearcutting produced a comparable level of songbird richness as shelterwoods, however, clearcuts had a higher proportion of early-successional songbird species than shelterwoods, which supported more forest species (Yamasaki et al., unpublished results). This is consistent with the findings of other studies in the region (e.g., DeGraaf, 1991; King and DeGraaf, 2000) that the effect of management activities varies in proportion to the magnitude of the alteration of the vegetation. Although partial cutting retains a larger proportion of the bird species characteristics of intact forest, the use of partial cutting exclusively would result in the decline of several species that were exclusively found in either mature forest or clearcuts, and would consequently result in a decrease in species diversity at the landscape scale (DeGraaf and Chadwick, 1987; King and DeGraaf, 2000). Based on their observations, Yamasaki et al. (unpublished results) recommended a variety of silvicultural techniques to maintain avian species diversity across forested landscapes in New England.

3. Fragmentation issues in forested landscapes

At the time bird research was initiated on the Bartlett Experimental Forest, the potential for forest management to fragment habitat in forested landscapes in the northeast U.S.A. was unknown, because the only studies on this topic were from the Midwest or Mid-Atlantic States where forest patches are isolated by agricultural or suburban development (e.g., Gates and Gysel, 1978; Whitcomb et al., 1981; Wilcove, 1985; Temple and Carey, 1988). Predation rates on both natural and artificial nests have been shown to be higher in small than in large fragments and are influenced by the distance to the forest edge (Gates and Gysel, 1978; Ambuel and Temple, 1983). Elevated nest predation rates have therefore been proposed as indicators of forest fragmentation (Whitcomb et al., 1981). Landscape-level reductions in avian nesting success associated with forest fragmentation are largely the result of changes in abundance and distribution of nest predators and brood parasites (Donovan et al., 1995; Robinson et al., 1995). Their abundance increases in fragmented landscapes because of increases in food resources associated with agricultural or suburban development (Wilcove, 1985; Andren, 1992). Their distribution changes in fragmented landscapes as nest predators invade forest edges from surrounding non-forest habitats that have more abundant food resources (Angelstam, 1986), or as nest predators concentrate near edges because of increased structural heterogeneity or plant

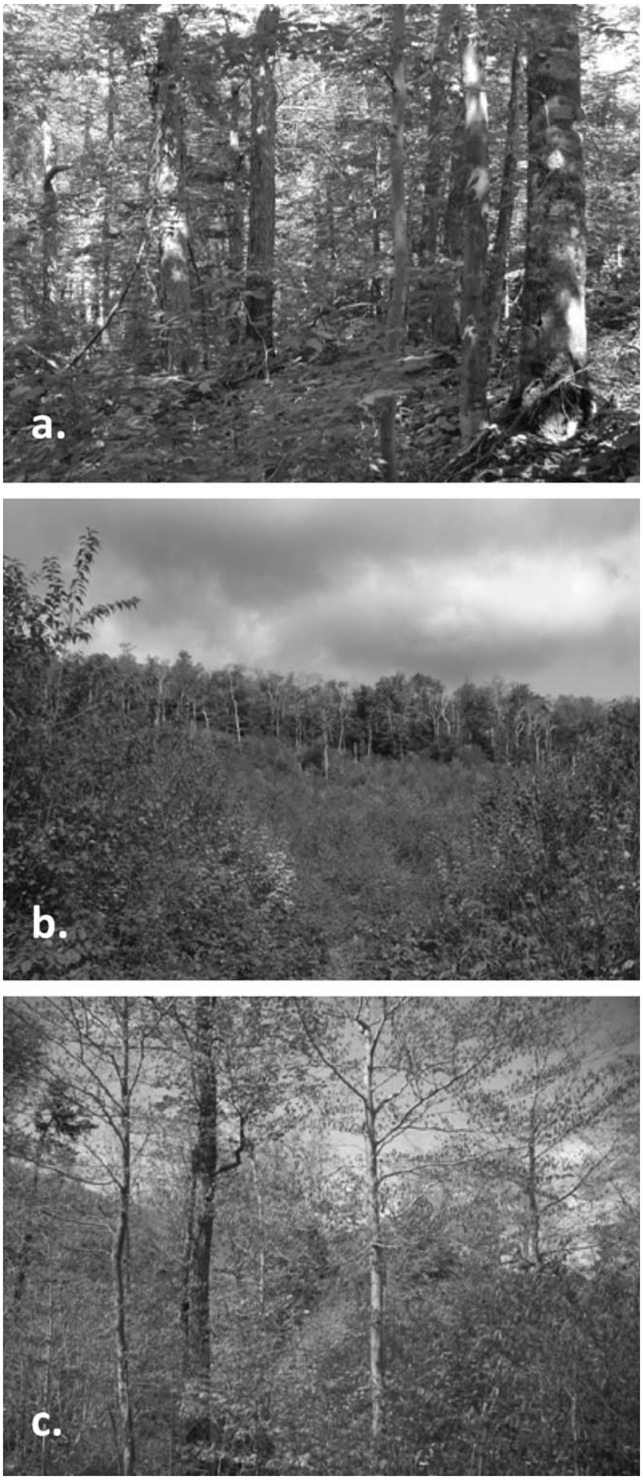

Fig. 2. Images of unmanaged forest (a.), a clearcut 7 years post-harvest (b.), and a shelterwood 9 years post-harvest (c.) on the Bartlett Experimental Forest, Bartlett, New Hampshire, U.S.A.

species composition near edges (Forsyth and Smith, 1973; Gates and Gysel, 1978; Chasko and Gates, 1982).

These explanations of changes in nest predator and brood parasite abundance and distribution are predicated on disturbances that provide non-forest habitat with abundant food resources, and that persist long enough to result in increased vegetative structure or changes in floristic composition near edges. The results of these studies are not necessarily applicable to extensively forested landscapes where forest is not isolated (DeGraaf and Healy, 1990) and where resources that support inflated numbers of nest predators and brood parasites in agricultural and suburban habitats are absent (King et al., 1997). Edges between even-aged northern hardwood stands, even of greatly contrasting age or height, are different from field-forest edges (DeGraaf, 1992). Foliage profiles in stands of widely disparate ages are similar, and effects of boundaries between even-aged stands on breeding birds are ephemeral. Vegetation in northern hardwood openings regenerates to a height of ~5 m within a decade (McClure et al., 2000), which restricts light penetration and growth of a brushy border (King et al., 1996). Thus, there are no unique species or assemblages between different-aged forests sampled in extensively forested areas in New Hampshire (DeGraaf, 1992). Similarly, King et al. (1997) reported that there was no evidence that forest birds avoided clearcut borders.

Research on the Bartlett Experimental Forest has been directed at assessing the potential for forest management to result in forest fragmentation. Although reductions in nesting success as a result of changes in landscape composition or increases in amount of edge may decrease the viability of forest bird populations (Temple and Carey, 1988; Thompson, 1993; Donovan et al., 1995), in the area surrounding the Bartlett Experimental Forest the primary source of forest disturbance is small scale clearcutting, which produces essentially no isolation, reverts quickly back to forest, and does not provide the habitat or food subsidy for potential nest predator species typically associated with agricultural or suburban habitats. Thus, it was unclear whether the findings of studies of nest predator response to edges from fragmented landscapes with significant human development apply to extensively forested landscapes consisting of forest and scattered clearcuts, although subsequent research has shown that nest success is lower for some bird species near clearcut borders than in forest interiors (King et al., 1996; Flaspohler et al., 2001; Manolis et al., 2002). DeGraaf (1995) reported that depredation rates on artificial ground and shrub nests monitored by trip cameras were similar between managed and reserved forest blocks. Elevated nest predation rates are generally considered to be indicative of fragmented forest conditions, so the results of this study suggest that extensive northern hardwood forests in northern New England are not fragmented by even-aged silviculture with clearcut regeneration. This finding is subject to the biases associated with artificial nests, which may not reflect patterns of nest predation on actual birds' nests (King et al., 1999), however, it is supported by the fact that nest survival rates on ovenbirds (*Seiurus aurocapilla*) on the Bartlett Experimental Forest (0.45 probability of fledging young; King and DeGraaf, 2002) are nearly twice as high as ovenbird nest survival rates in fragmented forests in the Midwestern U.S.A. (0.26 probability of fledging; Donovan et al., 1995). Thus, managers are obligated to consider the effects of forest management activities in their management plans, yet to the extent that Midwestern and mid-Atlantic systems differ from forested landscapes in the northeastern U.S.A., comprehensive assessments of these management activities based on research from fragmented landscapes will be ineffective.

3.1. *Distribution of brown-headed cowbirds*

A conspicuous component of more fragmented systems is the presence of brown-headed cowbirds (*Molothrus ater*), which are social brood parasites that lay their eggs in the nests of other bird species, reducing their reproductive success through the removal of host eggs and competing with host nestlings. Most research describing the potential effects of cowbirds on other birds has been conducted in landscapes where agricultural habitats favored by cowbirds are abundant and forest cover is a minor landscape component (Yamasaki et al., 2000). Managers in extensively forested landscapes of the northeast U.S.A. require information on how forest management activities affect cowbird numbers and their potential to impact native bird communities. Yamasaki et al. (2000) conducted surveys on the Bartlett Experimental Forest and surrounding areas. Of 365 observations of cowbirds, 361 of these were outside the boundaries of the White Mountain National Forest where agricultural and residential habitats comprised 27% of the land cover. In contrast, only 4 cowbirds were detected in areas within the boundaries of the White Mountain National Forest, which was 98% forested. Nesting studies conducted on the White Mountain National Forest during the same general time period (King et al., 1996, 2001; Chandler et al., 2009a) report rates of cowbird parasitism < 1%, indicating that the low abundance of cowbirds reported by Yamasaki et al. (2000) also reflected a generally low level of parasitism on actual nests. The findings by Yamasaki et al. (2000) provided managers with some assurance that unlike findings in more fragmented regions of the country, management activities on the White Mountain National Forest are unlikely to result in any elevation of risk of cowbird parasitism.

3.2. *Nest predator species composition*

Another contribution to ornithological research from the Bartlett Experimental Forest concerns the identification of nest predators species using videography (King et al., 2001; King and DeGraaf, 2006). Regional variation in nest predator communities is thought to be responsible for the variation in predation pressure associated with habitat fragmentation (e.g., Robinson et al., 1995). This regional variation is apparent in the predators recorded on video at bird nests. For example, snakes and ants have been reported to be important nest predators in the central and southern United States (Thompson et al., 1999; Stake and Cimprich, 2003; Stake et al., 2004), but these predators were not observed in the northwestern United States (Liebezeit and George, 2002). To date, few studies involving the use of video cameras have been conducted in the northeastern United States. Nest predation is an important cause of avian nest failure (Ricklefs, 1969), and elevated rates of nest predation can potentially compromise the viability of forest bird communities (Donovan et al., 1995).

The effect of management on bird populations is most directly manifested through changes in predation rates, yet except for anecdotal information and data from artificial nests, neither of which yield accurate data about actual predators (King et al., 1999), we do not know which predator species are responsible for depredating nests. The lack of information about the identity of nest predators may confound efforts to understand or predict the effects of habitat conditions or management activities on bird populations. For example, squirrels and chipmunks are thought to be important nest predators (Sloan et al., 1998), and higher rates of nest predation near edges in northern New England (King et al., 1996, 1998a) have been attributed to this greater concentration of sciurids in these habitats (King et al., 1998b). Prior to the advent of compact video monitoring technology, however, it has not been possible to verify what predator species are responsible for most nest predation. In the absence of this information, the mechanism actually responsible for edge-related nest predation in northern New England remained unknown.

King and DeGraaf (2006) identified nest predators on the Bartlett Experimental Forest using a video methodology of their own design (King et al., 2001), and found that the diversity of nest predators at their site (4 species) was similar to the median number of predator species detected on 13 published studies from North America (5 species). Mice and raptors were detected more frequently at the Bartlett Experimental Forest than in other published studies (King and DeGraaf, 2006). Their results indicate a variety of potential nest predators exist in northern New Hampshire and that, as a result, analyses of possible relationships between nest predation and habitat characteristics will be more difficult than if there were a single dominant predator. Because different predators differ in their search strategies and in the sensory cues used to locate nests, birds nesting in hardwood forests in New Hampshire may not be able to select nest sites that will provide security from all predators (Liebezeit and George, 2002). This combination of a diverse predator community and predator-specific differences in sensory abilities, periods of activity, and hunting methods might be responsible for the conflicting results among studies concerning the importance of nest site characteristics in influencing predation rates (Pietz and Granfors, 2000).

3.3. *Effect of forest roads on birds*

The creation of forest roads is another standard component of forest management, and has come under increasing scrutiny in recent years as a result of its perceived effects on forest health. Forest roads can potentially have a number of harmful effects on forest health, including the disruption of natural hydrological processes, increased erosion, or the facilitation of the invasion of forest interiors by exotic plants (Forman, 1998; Trombulak and Frissell, 2000). Recent studies indicate that forest roads can affect the distribution of forest birds. Rich et al. (1994) in New Jersey found that several forest bird species were less abundant near forest roads than in forest interiors. Similarly, Ortega and Capen (1999) reported that ovenbirds were less abundant near forest roads than in areas away from roads.

King and DeGraaf (2002) studied the effects of maintained and unmaintained forest roads on the Bartlett Experimental Forest to determine whether forest roads affected forest bird nest success, habitat or microclimate. They found that nest survival was actually higher within 0–75 m of maintained roads than >75–150 m away, which they attributed to avoidance of roadside areas by predators or improvements in some unmeasured habitat conditions not included in the analyses. They concluded that small, unsurfaced forest roads at low road density do not result in decreases in forest passerine bird productivity in extensively forested areas in New England.

The absence of increased nest predation near roads on the Bartlett Experimental Forest may be attributable to the fact that the roadsides there differ from other types of edges near which nest predation rates has been found to be higher. For example, permanent edges adjacent to agricultural or suburban development may develop vegetation structure distinct from areas away from edges that may concentrate nest predators (Gates and Gysel, 1978). Furthermore, food resources that may attract nest predators to edges adjacent to suburban or agricultural development, such as waste grain or garbage, are absent in the roadways we studied. Rich et al. (1994) reported greater brown-headed cowbird abundance near roads, especially roads with grassy shoulders. In forested landscapes such as northern New England, cowbirds are scarce (Yamasaki et al., 2000), and therefore the facilitation of cowbird invasion of forest areas in landscapes such as the White Mountain National Forest is not likely an important factor affecting avian reproductive success. In contrast, the construction of roads in regions where cowbirds are abundant might facilitate the invasion of interior forest by these brood parasites (Gates and Evans, 1998). Decreases in invertebrate food resources appear to affect the distribution and reproductive success of forest birds in fragmented landscapes (Burke and Nol, 1998; Zanette et al., 2000). Unlike edges in fragmented landscapes, the roads on the Bartlett Experimental Forest do not create large gaps in the canopy and were not associated with changes in microclimate (King and DeGraaf, 2002) as reported from fragmented landscapes (Burke and Nol, 1998; Zanette et al., 2000).

4. Shrubland birds

4.1. Habitat selection and management for shrubland birds

Many shrubland bird species are declining in eastern North America and as a result have become the focus of substantial conservation concern (Askins, 1993; Brawn et al., 2001; Hunter et al., 2001). These declines are associated with large-scale land use changes over the last century as mature forests have replaced old fields (DeGraaf and Miller, 1996; Litvaitis, 1993), and the use of even-aged silviculture has decreased (Trani et al., 2001; Oehler, 2003). In addition, the region's natural disturbance regime has been disrupted by fire suppression, flood control, reduction of beaver (*Castor canadensis*) populations, and establishment of younger forests that are more resistant to wind events (Lorimer, 2001; DeGraaf and Yamasaki, 2003; Chandler et al., 2009b). Thus, it is the view of many conservationists that active management will be needed to conserve these species (Hunter et al., 2001; DeGraaf and Yamasaki, 2003).

Clearcutting provides the early-successional habitat required or utilized by a variety of songbirds (DeGraaf, 1991; Costello et al., 2000; King and DeGraaf, 2000). Numerous studies have examined patterns of community change over successional time, documenting for example that species bird species diversity increases during secondary succession in forests (e.g., Johnston and Odum, 1956; Shugart and James, 1973; May, 1982). These patterns in community structure are in part the result of the restriction of individual species to certain seral stages. For example, in northern hardwoods forests, the bird community undergoes almost 100% species turnover from stand initiation to stand maturity (DeGraaf, 1991). Although the period of time over which clearcuts provide habitat for shrubland birds is known from studies assembling chronosequences from different-aged sites (DeGraaf, 1991; Schlossberg and King, 2009), an inherent assumption of these studies is that the characteristics of the individual sites combined yields the same information as if individual sites were actually followed through time. Long-term data with which to test this assumption are uncommon; however, Yamasaki et al. (unpublished results) surveyed breeding birds at two sites on the Bartlett Experimental Forest from 1999 through 2007 and showed that early-successional species began to occupy the clearcut in the first growing season and became the majority component of the bird community by the third growing season, maintaining that position until the seventh growing season. Generalists/later-successional species were the majority component of the bird community in the low-density shelterwood throughout the study. Numbers of early-successional individuals far outweighed generalists/later-successional individuals in the clearcut throughout the study; while the number of generalists/later-successional individuals comprised the majority in the low-density shelterwood throughout the study. These observations generally confirmed the results of other studies based on chronosequences, and provide managers with information needed to inventory and manage habitat for shrubland birds.

4.2. Area sensitivity of shrubland birds

It is clear from the foregoing that clearcutting is an effective technique for creating habitat for shrubland birds (DeGraaf, 1991; Thompson et al., 1992; King and DeGraaf, 2000; Yamasaki et al., unpublished results), however, comparatively little information exists on avian responses to patch size. Clearcutting is the most common method of even-aged management practiced on the White Mountain National Forest, and although it is an efficient method for regenerating many tree species (Leak et al., 1997), and is an effective means of providing wildlife habitat (Hunter, 1990; DeGraaf et al., 2006), the use of clearcutting has been reduced significantly on public lands. Reasons for this reduction are mainly due to public sensitivity to the visual impact of clearcuts and perceived detrimental effects to wildlife habitat and forest health. This criticism has led to increased utilization of uneven-aged silvicultural practices, such as group selection on the White Mountain National Forest. Under this system, groups of two or more adjacent trees are removed from the forest overstory at intervals ranging from 10 to 20 years. The size of these openings ranges from 0.05 to 0.80 ha depending on management objectives. If group selection were to replace clearcutting as the predominant silvicultural technique, managed forest openings on the White Mountain National Forest will be limited to 0.80 ha in size. Previous studies have focused on the minimum size of forest fragments required to support songbirds that breed in mature stands (Galli et al., 1976; Ambuel and Temple, 1983; Robbins et al., 1989); however, information is lacking on the area sensitivity of species requiring early-successional habitat. The size of a forest opening may be an important feature with respect to breeding bird composition; evidence to support this has been described by Rudnicky and Hunter (1993) who found an increase in species richness with an increase in clearcut size up to 20 ha. Information is also sparse on the communities that utilize the uncut forested portions of a group selection stand.

To provide an evaluation of the potential for group selection to provide habitat for shrubland birds, Costello et al. (2000) surveyed forest openings on the Bartlett Experimental Forest and environs and found that species richness was significantly higher in clearcut openings than in group selection openings, and that a number of species found in clearcuts were scarce or absent in group selection cuts. They concluded that, relative to avian use, the group selection system does not provide habitat similar to that created by clearcutting in extensive northern hardwood stands. The group selection system appears to retain much of the mature forest bird community while providing for a limited number of early-successional bird species. Gradual replacement of clearcutting with group selection harvests could result in reduced avian diversity across large forested tracts. These results have important implications for forest managers seeking to provide bird habitat during the course of management activities.

5. Post-fledging ecology—habitat selection and habitat-specific survival

5.1. Species-specific patterns

Relatively little attention has been given to the post-fledging period (the period of time between fledging and the onset of migration), which might also have an important influence on migrant populations. Studies of parids (Dhondt, 1979; Perrins, 1980; Naef-Daenzer et al., 2001), the European blackbird (*Turdus merula*; McGrath, 1991), the yellow-eyed junco (*Junco phaeonotus*; Sullivan, 1989) and the Florida scrub jay (*Aphelocoma c. coerulescens*; Woolfenden, 1978) all indicate that mortality is indeed heavy during this period. One aspect that is almost entirely lacking from these studies is the habitat use of fledgling birds during the period between leaving the nest and independence, and its relationship to survival. The reason for this oversight is probably related to the fact that until relatively recently, studies of this nature had to rely on capture–recapture models of birds banded as nestlings; hence opportunities to resight juvenile birds and evaluate their habitat use were limited. This has changed with the development of lightweight radio transmitters, which have permitted a quantum leap in our understanding of the ecology of bird species during this period.

Patterns of habitat selection by nesting adults of many bird species are relatively well understood; however, recent studies indicate that the habitat preferences of some forest birds change after the young fledge from the nest. For example, studies indicate that wood thrush fledglings move from nest sites in mature forest into stands of dense vegetation in which they stay for extended periods of time until they migrate (Anders et al., 1998; Vega Rivera et al., 1998). Moreover, fledgling survival rates are relatively low during the time period between fledging and when they reach these areas with dense vegetation, but increase dramatically thereafter (Anders et al., 1998). This last point is especially important in light of studies suggesting that bird populations are particularly sensitive to mortality during the post-fledgling period (Perrins, 1980; Kurzejeski and Vangilder, 1992), suggesting that this parameter has a potentially important influence on population dynamics in at least some bird species.

To address the lack of information on the post-fledging period, King et al. (2006) studied ecology of fledging ovenbirds on the Bartlett Experimental Forest using radio telemetry and found that habitat at sites used by radio-marked fledgling ovenbirds was characterized by fewer large trees and greater vertical structure 0–3 m above ground than ovenbird nest sites. Similarly, habitat at sites used by fledgling ovenbirds was characterized by fewer large trees and greater vertical structure than unused sites. Most (80%) of the 15 mortalities that we observed were due to predation. Nine (70%) of these occurred within the first 3 days of fledging, resulting in a significant drop in survival during this period. Fledgling survival increased significantly with increased vegetation structure. Chandler (2006) did a similar study on the Swainson's thrush (*Catharus ustulatus*) and found similar patterns. These observations that fledgling birds are selective in their habitat use, that they select different habitat features than adult ovenbirds select for nesting and that fledgling survival is positively associated with these habitat features suggest that the use of habitat models based on counts of singing males before fledging does not adequately represent the habitat needs of this species. Conceivably, mortality during the post-fledging period could limit recruitment to levels insufficient to maintain the viability of ovenbird population even if adequate nesting habitat were available.

5.2. Community-level patterns

Additional work at the Bartlett Experimental Forest using both point counts and mistnetting in regenerating clearcuts, recently treated wildlife openings, and adjacent mature forest showed that a number of migratory songbirds that nest in mature forests were found in higher densities in early-successional forests than mature forests during the post-fledging period, and that species assemblages differ between clearcuts and wildlife openings (Chandler, 2006). Additionally, these species occur in highest densities in large clearcuts with tall, complex vegetation structure and large wildlife openings with tall vegetation and the presence of standing dead vegetation. These attributes may provide protective shelter from predators when birds are most vulnerable, or offer higher food abundance than mature forests.

5.3. Summary and conclusion

Birds are ecologically important and highly valued by the American public. Reliable knowledge on the effect of management on their populations is vital to their conservation. Three decades of avian research conducted at the Bartlett Experimental Forest has provided information on habitat management for birds. For example, research from the Bartlett Experimental Forest quantified avian use of snags and coarse woody debris, which have provided the basis for guidelines for the management of this important habitat feature. Early work on the effects of silviculture on birds also took place on the Bartlett Experimental Forest, which highlighted the limitations of uneven-aged silviculture for managing birds. Research at the Bartlett Experimental Forest also provided information for managers on the degree to which silviculture causes fragmentation, which indicated that levels of nest predation and parasitism included by management probably have a negligible effect on bird populations in the region. Shrubland birds are the subjects of considerable conservation concern, and research at the Bartlett Experimental Forest has highlighted the habitat specialization of this group, which dominates regenerating clearcuts for only a decade after treatment. This research has also shown that some shrubland birds are sensitive to habitat area, similar to findings for mature forest birds in fragmented landscapes. Finally, recent research on the Bartlett Experimental Forest has provided new insights into the importance of the post-fledging period. Telemetry studies showed fledging ovenbirds select habitat that confers higher survival, and that many species of mature forest birds are more abundant in early-successional habitats than mature forest. All of this work was greatly facilitated by the dedication of the Bartlett Experimental Forest to long-term, interdisciplinary research, as well as control over treatments and access to laboratory and dormitory facilities.

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