Effects of timber harvests on invertebrate biomass and avian nest success

by Jeffrey P. Duguay, Petra Bohall Wood, and Gary W. Miller

Abstract Concerns over declining songbird populations have led to investigations of effects of various timber management practices on breeding songbirds. We assessed the influence of 2 types of practices, two-age and clearcutting, on invertebrate biomass and avian daily nest survival in the Monongahela National Forest of West Virginia during summers of 1995 and 1996. We also examined relationships between invertebrate biomass, avian daily nest survival, and wood thrush (*Hylocichla mustelina*) nestling growth rates. Mean total invertebrate biomass collected per sample day and litter-dwelling invertebrates collected per sample day were 0.0614 g and 0.0254 g greater ($P \leq 0.10$), respectively, in the unharvested than clearcut treatment late in the season (2 Jun to 12 Jul) when most birds had young in the nest; whereas invertebrates that hide under tree bark during the day had greatest biomass ($P=0.003$) in the two-age treatment during this same time period (0.1355 g greater than clearcut and 0.0616 g greater than unharvested). In addition, daily nest survival rates (216 nests) were greater in the unharvested than two-age treatment ($P \leq 0.05$). The lesser daily nest survival rates of birds breeding in the harvested treatments may be due to increased predator activity within these areas and/or reduced food supplies. Significant positive correlations between invertebrate biomass and daily nest survival rates of breeding birds and faster growth rates of wood thrush nestlings in stands with a greater invertebrate biomass suggest that changes in invertebrate biomass caused by silvicultural practices have an influence on breeding birds within these areas.

Key Words insect biomass, nest predation, nest survival, silviculture, timber management

Concern over declining populations of songbirds has led to considerable research on the effects of timber management on songbirds during the breeding season. Studies have revealed that relatively small cuts in otherwise extensively forested areas may displace a few forest-interior bird species, but such cuts also may increase the diversity and abundance of breeding birds (Derleth et al. 1989, Thompson et al. 1992, Welsh and Healy 1993). Investigators have concluded that such timber management activities are not detrimental to breeding birds.

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However, population density may be a poor indicator of habitat quality (Van Horne 1983, Vickery et al. 1992). At greater densities, songbirds can have reduced reproductive success (Arcese and Smith 1988, Vickery et al. 1992).

In addition to examining the numerical response of breeding birds to timber management practices, investigators have conducted studies using artificial nests to discern what influence these practices may have on predation rates. Trends in predation rates on artificial nests often are related to those expected on nests of breeding birds (Andren 1992, Leimgruber et al. 1994, DeGraaf 1995). However, artificial-nest studies may underestimate predation rates (Haskell 1995*a*). Given that density may be a misleading indicator of habitat quality and that artificial-nest studies may not accurately portray predation rates on breeding birds, it is necessary to investigate nest predation rates on breeding birds in areas harvested using different types of silvicultural practices.

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A factor generally overlooked when examining the influence of timber management practices on breeding birds is how such practices affect food availability. Changes in habitat structure have caused changes in assemblages and abundance of invertebrates (the primary food source of breeding birds) (Schowalter et al. 1981, Niemela et al. 1993). Because studies have suggested that birds are food-limited during the breeding season (Martin 1986, Duguay 1997), it is important to determine what impact timber management practices have on invertebrates and how breeding birds are affected by these changes in food supplies.

Although birds may be food-limited during the breeding season and timber management practices have been shown to impact invertebrate communities, we do not know of any published studies that have simultaneously investigated the effects of different types of silvicultural practices on invertebrate biomass and breeding success of birds. Our objectives were to determine whether, approximately 15 years after harvest, different silvicultural practices (two-age and clearcut) influenced invertebrate biomass and daily nest survival rates of breeding birds and whether invertebrate biomass influenced avian daily nest survival and nestling growth rates.

Study area

We conducted this study on 18 forest stands in the Monongahela National Forest (MNF). The MNF is located within the Allegheny Mountains region of West Virginia and encompassed over 364,225 ha. The topography consisted of low valleys dissected by northeast–southwest ridges (United States Forest Service 1986). Elevations of our study sites ranged from 779 m to 1,472 m above sea level. Dominant tree species consisted of black cherry (*Prunus serotina*), black birch (*Betula lenta*), yellow poplar (*Liriodendron tulipifera*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), fire cherry (*Prunus pensylvanica*), sassafras (*Sassafras albidum*), and sourwood (*Oxydendrum arboreum*, Nichols 1996).

Clearcutting involves removal of an entire stand in one cutting (Thompson et al. 1992) and is a commonly used silvicultural method. However, because of public concern over clearcutting, alternatives such as two-age management have been investigated with some positive results from a forest management perspective (Smith et al. 1989, Miller et al. 1995). Two-age stands resemble a seed-tree cut with 37–49 mature trees/ha remaining. However, when the regenerated stand becomes established, residual trees are not harvested but rather remain until the new stand reaches rotation age (Smith et al. 1989).

Twelve stands were harvested using the two-age or clearcut method and 6 were unharvested. Mean size of the 6 two-age stands was 5.1 ha (range 4–7 ha); mean size of the 6 clearcut stands was 6.4 ha (range 4–11 ha). Two-age stands were harvested between 1979 and 1986 and clearcut stands between 1980 and 1982. The 6 unharvested stands were 75 to 85 years old. We used a spatial analysis program (FRAGSTATS, McGarigal and Marks 1995) to calculate the mean percentage forest cover, mean core forest area, and mean size of agricultural and urban areas within a 7-km radius of the center of each treatment on a 1993 land-cover map. Mean core forest area was defined as a forest patch with a 100-m buffer from the forest edge in all directions.

Mean percentage forest cover was 90.0% for the two-age treatment, 89.0% for the clearcut treatment, and 92.1% for the unharvested treatment. Mean core forest area was 46.9 ha for the two-age treatment, 32.9 ha for the clearcut treatment, and 56.9 ha for the unharvested treatment. Mean patch size of agricultural areas was 1.3 ha for the two-age treatment, 2.3 ha for the clearcut treatment, and 0.6 ha for the unharvested treatment. Mean

patch size of urban areas was 0.4 ha for the two-age treatment, 0.2 ha for the clearcut treatment, and 0.6 ha for the unharvested treatment.

Methods

Nest searching

We searched intensively for nests to determine daily nest survival. We visited all nests found every 3–4 days to check status (i.e., incubation, brooding, or fledgling stage) and to document the fate of each nest. If at least one young fledged, we considered the nest successful. In determining nest contents, we used a mirrored pole to check those that were too high to see into. For nests that could not be reached with a mirrored pole, we used behavioral observations to determine the nesting stage.

To minimize the possibility of attracting predators to a nest location, we used flagging only when necessary to relocate a nest (Yahner and Wright 1985). If used, flagging was placed ≥25 m from the nest. All other nests were relocated by following descriptions in field notes. We used a different direction each time we approached a nest (Martin and Geupel 1993).

Nestling growth rates

In 1996, we measured the growth of wood thrush (*Hylocichla mustelina*) nestlings every 1 to 3 days at approximately the same time each day. We measured mass to the nearest 0.05 g using a 50-g Pesola spring scale and tarsus length to the nearest 0.1 mm using a dial caliper. We uniquely marked nestlings by coloring a different toe with a permanent marker, and each nestling, when old enough, was banded with a United States Fish and Wildlife Service aluminum band. Young were not handled after day 8 (hatch date=0), to avoid premature fledging. No young fledged while being handled.

Invertebrate sampling

We used 3 invertebrate sample methods (pitfall traps, burlap bands, and Malaise traps) to quantify invertebrate biomass on each study site during 1995 and 1996 (Duguay 1997). In each of the 18 stands we randomly placed 2 invertebrate sample stations. At each station, 9 pitfall traps (0.47–l plastic cups arranged in a 3 × 3-m grid) were one-fourth filled with propylene glycol and buried in the ground with the top edge level to the ground surface. We placed burlap stations with pitfall trap stations. Burlap bands (0.46 m in width) were placed at breast height primarily on *Acer* spp., *Betula* spp., *Prunus* spp., *Quercus* spp., and *Tilia* spp. in the early spring before leaf-out. Half of a 7.31-m (3.34 m^2) burlap roll was used at each station. We placed one Malaise trap within each stand at a randomly selected location and attached a jar filled approximately one-fourth with 70% ethanol.

We activated invertebrate sampling devices during the third week (1995) and fourth week (1996) of April. Once activated, invertebrate collection ran continually throughout the sampling period, which ended during the second week of July in both years. We collected invertebrate samples every 2 weeks from each of the 3 methods. In the laboratory, we sorted samples by order and size (<3 or ≥3 mm) and counted number of individuals. Biomass to the nearest 0.0001 g was measured after drying samples in a 50° C oven for 48 hours. We used invertebrate biomass as an index of food availability and not an absolute measure of food items consumed by breeding birds, as other investigators also have done (Newton 1980, Hutto 1985, Holmes et al. 1991, Barba et al. 1994).

Data analyses

We used the Statistical Analysis System (SAS Institute 1989) for all analyses. Because a conservative approach is often justified when examining factors causing population declines (Askins et al. 1990, Caughley and Gunn 1996), we considered differences significant at $P \leq 0.10$.

We calculated daily nest survival using the Mayfield method (Mayfield 1961, 1975). Variance (V) was estimated as V=survival × mortality/the number of days a nest was under observation (Darveau et al. 1993). We used the program CONTRAST (Hines and Sauer 1989) to compare daily nest survival estimates between treatments for all species combined and by foraging guild. When examining relationships between daily nest survival of all birds combined and invertebrate biomass, we excluded from analyses stands with fewer than 4 nests. We excluded all cavity nests.

We examined growth slope (mass and tarsus increase) during days 1–7. We determined growth slope for a nestling when mass was measured on at least 3 of the 7 days. Where food limits growth, only 1 to 2 nestlings in a brood of 4 might show retarded development (Rodenhouse and Holmes 1992). Thus, we examined growth rates of nestlings, rather than broods. We calculated linear growth slopes of nestlings because the increase in nestling mass was approximately linear during the period when weighing and measuring nestlings was possible (days 1–7). We used linear regression analysis to examine the influence of invertebrates on growth slopes. Because of small sample sizes, treatments were pooled for analyses.

We used a nested analysis of variance (ANOVA) to examine mean invertebrate biomass collected/sample day between treatments and stands within treatments. One

trap active for one day was equivalent to one sample day. For analyses, we used the combined biomass collected at the 2 insect sample stations within each stand.

We examined invertebrate biomass to determine whether there were differences among treatments early (late Apr to 01 Jun) and late (02 Jun to 12 Jul, when most birds had young in the nest) in the season. In late May 1995, 5 of the 6 clearcut stands were sprayed with the insecticide *Bacillus thuringiensis* (BT), which is specific to larval Lepidoptera (Sample et al. 1996). We excluded the sprayed stands from the 1995 data during invertebrate analyses. Because insecticide spraying of clearcut stands nearly coincided with our late-spring invertebrate collection in 1995, we included all clearcut stands in the analyses for the early time period but not for analyses of the late time period.

We examined the relationship of invertebrate biomass on avian daily nest survival rates for all species pooled and by foraging guilds (ground gleaning, bark gleaning, and hawking) based on classifications by Ehrlich et al. (1988) using Pearson product-moment correlation. We used total invertebrate biomass (excluding unpalatable orders; Chilopoda, Diplopoda, Pseudoscorpionida) to examine all bird species pooled. We used invertebrates collected by pitfall traps to examine the relationship of invertebrate biomass on ground gleaner daily nest survival rates. We used invertebrates collected under burlap bands to examine the relationship of invertebrate biomass on bark gleaner daily nest survival. Invertebrates collected by Malaise traps were used to examine the relationship of invertebrate biomass on flycatcher daily nest survival rates.

Results

Invertebrates

Mean invertebrate biomass for all collections, taxa, and collection methods combined increased ($F_{2,45}$=5.53, P=0.007) from early to late in the season in the two-age (increase of 0.0226 g/sample day) and unharvested treatments (increase of 0.0485 g/sample day), but declined in the clearcut treatment (decline of 0.0299 g/sample day, Figure 1). Invertebrate biomass did not differ among treatments early in the season for all collections, taxa, and collection methods combined or by individual collection method (P>0.10). Mean invertebrate biomass was least ($F_{2,9}$=3.09, P=0.08) in the clearcut treatment late in the season (two-age=0.0792 g, clearcut=0.0376 g, unharvested=0.0990 g, Figure 2).

We compared invertebrate biomass between treatments for each foraging guild late in the season when most birds had young in the nest. Mean biomass of invertebrates captured in pitfall traps was least ($F_{2,9}$=3.29, P= 0.07) in the clearcut treatment late in the season (two-age =0.0162 g, clearcut=0.0123 g, unharvested=0.0377 g, Figure 2), whereas mean biomass of invertebrates collected under burlap bands, likely food items for bark gleaners, was greatest ($F_{2,9}$=4.76, P=0.03) in the two-age treatment (two-age=0.2417 g, clearcut=0.1062 g,

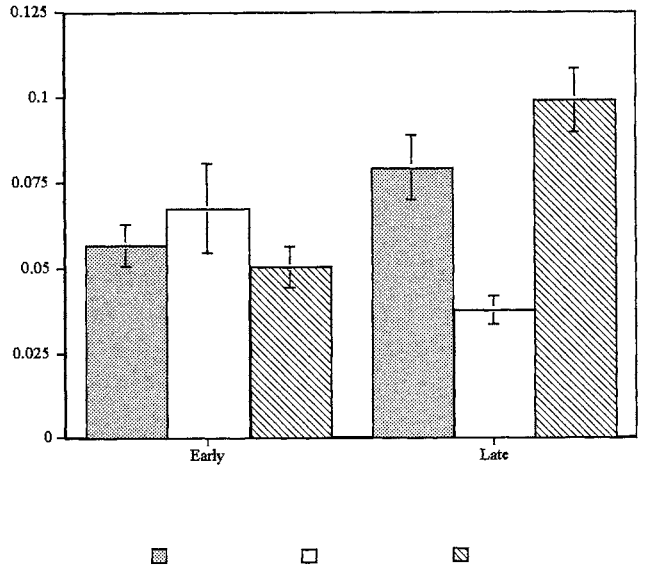

Figure 1. Change in invertebrate biomass per sample day by treatment and collection method from early (late Apr to 1 Jun) and late (2 Jun to 12 Jul) in the season. Vertical lines represent SE.

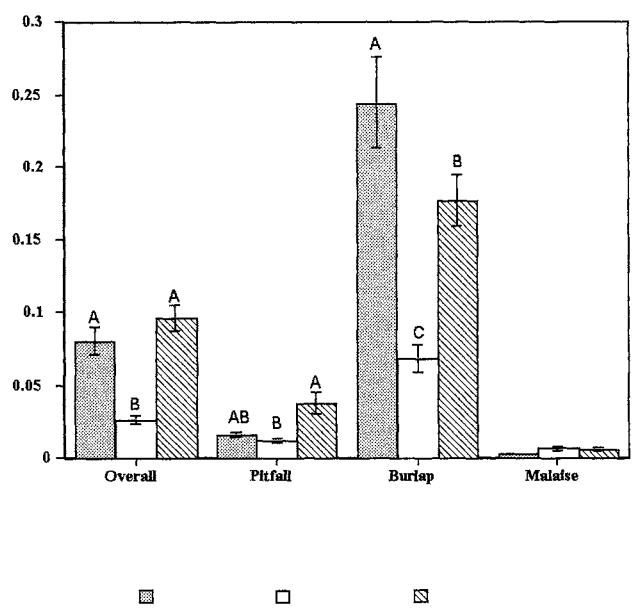

Figure 2. Mean invertebrate biomass per sample day by treatment and collection method late in the season, Monongahela National Forest, West Virginia, 1995 and 1996. Overall = mean invertebrate biomass per sample day, all collection methods combined; pitfall = pitfall biomass; burlap = burlap biomass. Within a group, bars with the same letter do not differ (P > 0.10). Vertical lines represent SE.

Table 1. Daily nest survival rates and percentage nest success for birds breeding on the Monongahela National Forest, West Virginia, 1995 and 1996.

	Number of nests	Daily survival[a]	Daily variance	Percentage success
All guilds				
Two-age	63	0.959 B	0.00005	32.1
Clearcut	43	0.959 AB	0.00008	32.5
Unharvested	110	0.974 A	0.00002	49.0
Ground-gleaners				
Two-age	33	0.962	0.00008	41.9
Clearcut	22	0.960	0.00015	40.0
Unharvested	33	0.970	0.00009	50.0

[a] Means with the same letter do not vary significantly.

unharvested=0.1801 g, Figure 2). Biomass of invertebrates captured in Malaise traps did not vary among treatments ($F_{2,9}$=1.00, P=0.39) late in the season (Figure 2).

Nest survival

During this 2-year study, we monitored 216 active nests. Predation was the primary cause of nest failure (85% of 91 failed nests). Daily nest survival for all bird species combined (Table 1) was greater (χ^2_2=7.80, P= 0.02) in the unharvested than two-age treatment.

Daily nest survival did not vary among treatments for ground gleaners (χ^2_2=1.89, P=0.39) (Table 1). Small sample sizes did not permit examination of daily nest survival rates for birds that forage by bark gleaning (2 nests, both successful) or hawking (15 nests, all in the unharvested treatment).

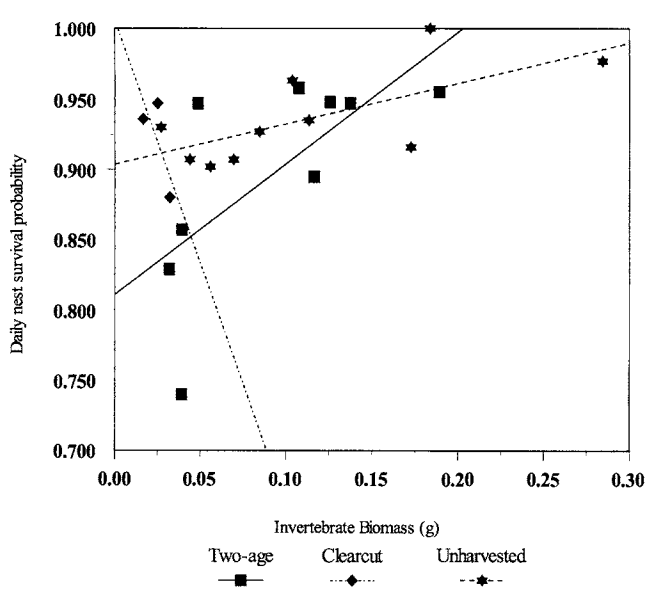

Figure 3. Daily nest survival probabilities for all bird species combined and mean invertebrate biomass (g) per sample day late in the season, Monongahela National Forest, West Virginia, 1995 and 1996.

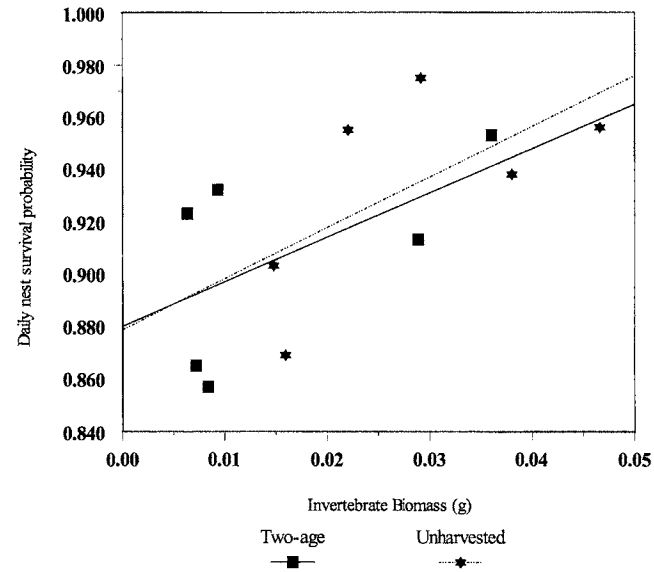

Figure 4. Daily nest survival probabilities for ground gleaners and mean pitfall biomass (g) per sample day late in the season, Monongahela National Forest, West Virginia, 1995 and 1996.

Invertebrate biomass and daily nest survival rates

Sample sizes were sufficient to examine correlations between invertebrate biomass and daily nest survival rates for all bird species combined and ground gleaners. Late-season invertebrate biomass and daily nest survival rates for all bird species combined for the two-age and unharvested treatments were correlated positively (r= 0.73, P=0.03; r=0.63, P=0.05; respectively) (Figure 3). Invertebrate biomass and daily nest survival rates for birds nesting within the clearcut treatment were not correlated (r=–0.69, P=0.51).

Invertebrate biomass in pitfall traps and daily nest survival rates of ground gleaners nesting were not correlated (r=0.63, P=0.18, r=0.58, P=0.22; respectively) in the unharvested or two-age treatments (Figure 4). We located too few nests of ground gleaners in the clearcut treatment to test for correlations.

Nestling growth rates

Total invertebrate biomass collected during the nestling stage and growth slope of wood thrush nestling mass and growth slope of wood thrush nestling tarsus (R^2= 35.0, P=0.02; R^2=34.0, P=0.02; respectively) were positively related (Figure 5).

Discussion

Effects of treatments on invertebrate biomass

Invertebrate biomass did not differ among treatments early (Apr to 1 Jun) in the season but did later (2 Jun to

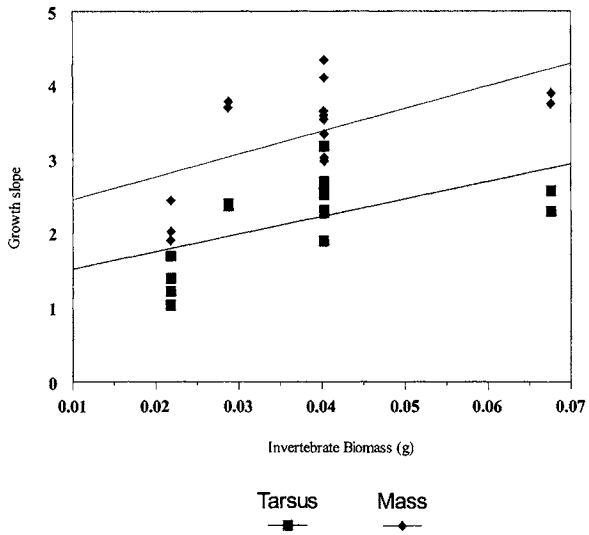

Figure 5. Mean invertebrate biomass per sample day and growth slope of wood thrush nestling mass and growth slope of wood thrush nestling tarsus.

12 Jul) in the season when many birds had young in the nest. Total invertebrate biomass increased from early to late in the season in the two-age and unharvested treatments, but declined in the clearcut treatment. This increase in biomass from early to late was probably from insect young being recruited into the population through fecundity (Adams 1941, Greenberg and McGrane 1996). Although we excluded stands sprayed with insecticide from analysis in the year when they were sprayed, the decline observed in the clearcut treatment may be due to insecticide application in 1995. The insect population likely was still reduced in 1996, so perhaps there were fewer adults to reproduce the following year in these stands.

Older forests generally contain a more diverse and abundant fauna of invertebrates than younger stands (Jolivet 1986), because older forests contain a wide diversity of plants, are slow growing, and offer a large selection of food sources of different ages, palatabilities, and nutritive qualities (Jolivet 1986, Niemela et al. 1993, Schowalter 1995). Studies in coniferous forests have shown lesser abundances of invertebrates in harvested than unharvested stands (Helle and Muona 1985, Niemela et al. 1993). Perhaps the same is true in deciduous forests. Thus, the greater biomass of invertebrates in the unharvested treatment may be attributable to the forest structure, long time periods that invertebrates have to coevolve in these areas, and a more favorable microclimate than harvested stands.

Differences in invertebrate biomass by capture method also were detected. Litter-dwelling invertebrates were most abundant in the unharvested treatment. Although percentage of litter cover did not vary among treatments, there was a greater percentage of high-canopy cover (≥12 m) in the unharvested treatment (Duguay 1997). The high-canopy cover may have provided a more favorable microclimate, such as cooler temperatures and increased soil moisture, for litter-dwelling invertebrates (Niemela 1990, Niemela et al. 1993, Greenberg and McGrane 1996).

Invertebrates captured under burlap bands were most abundant in the two-age treatment. It could be argued that invertebrates that hide under tree bark, which burlap bands mimic, were more abundant in the two-age treatment than the unharvested treatment simply because there were more trees with burlap bands (due to smaller trees) on them in the two-age than unharvested treatment. However, if true, then abundance should be greatest in the clearcut treatment because there were 60% more trees with burlap bands on them than in the two-age treatment (Duguay 1997). This suggests that number of trees with burlap bands on them is not influencing the amount of invertebrates collected under them.

The greater biomass of invertebrates under burlap bands in the two-age treatment may be related to vegetation structure. The two-age stands retain characteristics of mature forests and regenerating stands, including mature residual trees and abundant regenerating vegetation. Retaining mature trees may result in some taxa of invertebrates occurring in the two-age stands that were not found in the clearcut stands but do occur in mature forests. Additionally, some taxa of invertebrates are more abundant in harvested than unharvested stands (Greenberg and McGrane 1996). Thus, it may be this combination of characteristics, mature trees and regenerating vegetation, that resulted in the greater abundance of bark-dwelling invertebrates in the two-age treatment.

Avian reproduction and invertebrates

Invertebrate biomass at our study sites differed among treatments and likely impacts avian reproduction. Wood thrush nestlings in stands with a lesser invertebrate biomass grew at a slower rate than did wood thrush nestlings in stands with a greater biomass of invertebrates. Other studies also have shown that natural variation in food supplies influenced growth rates of nestlings (Price 1985, Dias and Blondel 1996, Holmes et al. 1996). Differences in nestling growth rates can have important consequences for breeding birds. Slower growth rates may cause a nestling to remain in the nest for a longer period of time, fledge at a lighter mass, or both. Predators often consume an entire brood when predating a nest (Rodenhouse 1986, Sullivan 1989, personal observation). Thus, when

Newly hatched veery chick and eggs. Photo by J. P. Duguay.

young remain in the nest longer, there is an increased likelihood of total nest failure. Because birds may reduce available food supplies throughout the breeding season (Holmes et al. 1979, Marquis and Whelan 1994, Gunnarsson 1996), young that fledge later may have lesser encounter rates with prey than those individuals fledging earlier. This may be especially important for fledglings that lack foraging proficiency and are susceptible to starvation once adults stop feeding them (Sullivan 1989).

Although positive correlations between invertebrate biomass and daily nest survival were detected, it is unclear what role, if any, food availability plays in avian daily nest survival. Perhaps invertebrate biomass and predator activity work in concert to produce differences in nest success among treatments. In areas with more food, adults may spend less time foraging, which increases the amount of time available for nest defense (Wolf et al. 1990, Martin 1992). Cresswell (1997) suggested that parental nest defense is the most important factor in reducing predation on eggs and nestlings. Indeed, studies have consistently shown predation to be the primary cause of nest failure (Gates and Gysel 1978, Bollinger and Linder 1994, Filliater et al. 1994). In addition, when more food is available, adults may be able to carry several food items to the young at one time, resulting in fewer trips to the nest, with fewer cues for predators. Thus, differences in invertebrate biomass among treatments may serve as an important factor in determining nest success. Birds breeding in areas with more available food may be able to spend more time near the nest (Arcese and Smith 1988), increasing the likelihood of detecting and possibly deterring a predator. However, both predator density and species of predator are likely to dictate the importance of invertebrates in influencing daily nest survival. In areas of great predator density, the probability that a predator will encounter a nest while a parent bird is away is greater than that in areas of lesser predator densities. In addition, a passerine may be unlikely to drive away a large predator such as a raccoon (*Procyon lotor*). Thus, in very fragmented areas where density of predators is typically greater than that of unfragmented forests (Haskell 1995*b*) and where large predators such as raccoons may be more abundant (Rodenhouse et al. 1995), the importance of invertebrates in dictating nesting success is likely to be of less importance than in unfragmented areas. If birds breeding in areas with more available food are able to spend more time in nest defense or provide predators with fewer cues to the location of the nest, then predation rates in these areas may be reduced. Studies that examine parental time and behavior at the nest and feeding rates in conjunction with food supplies are warranted to determine what influence food supplies have on nest predation rates.

Management implications

A goal of this study was to examine how two-age timber management impacted breeding songbirds and invertebrates compared to clearcutting and no-harvesting. No differences existed in avian daily nest survival between the two-age and clearcut treatments, but daily nest survival rates were greater in the unharvested than the two-age treatment. Total invertebrate biomass when most birds had young in the nest was greater in the two-age and unharvested treatments than in the clearcut treatment. Invertebrate biomass may mediate predation rates at the nest (Martin 1986), may influence reproductive parameters of breeding birds (Rodenhouse and Holmes 1992, this study), and may influence survival of birds after fledging (Sullivan 1989). Thus, from a songbird perspective,

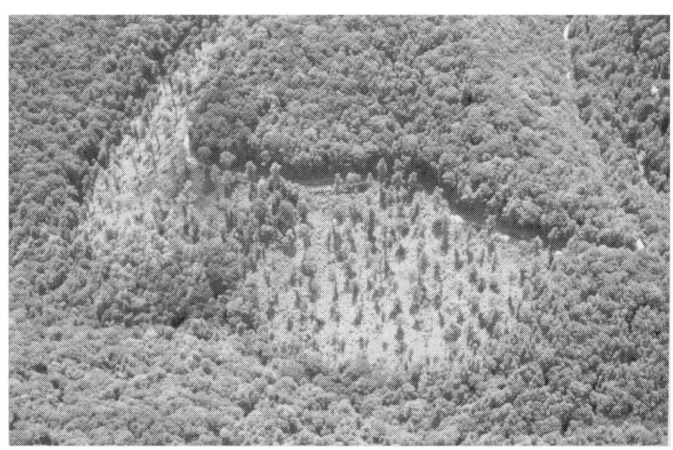

Figure 7. A two-age central Appalachian hardwood stand on the Fernow Experimental Forest, Parsons, West Virginia. The photo was taken in 1984 when the residual overstory trees were 83 years old and the new regeneration was 3 years old. Photo by J. N. Kochenderfer.

two-age timber management can be used as an alternative method to clearcutting within large tracts of mature forest.

However, daily nest survival rates were greatest in the unharvested treatment. Thus, if the management goal is to produce songbirds that do not rely on early successional habitat, then timber harvesting should be done in such a way that large tracts of mature forest are left intact.

It also must be remembered that this study was conducted approximately 15 years post-harvest in large forested tracts. During the first several years after a harvest, there is rapid regrowth and change in species composition and abundance of vegetation (Oliver and Larson 1996). Stands in a later stage of development, as in this study, remain stable for longer periods (Oliver and Larson 1996). Thus, invertebrate biomass and nest success probably differ to a greater extent shortly after a harvest than 15 years post-harvest. As such, results from this study should not be extrapolated to younger stands that are rapidly changing in vegetative structure or to very fragmented areas.

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Literature cited

ADAMS, R. H. 1941. Stratification, diurnal and seasonal migration of the animals in a deciduous forest. Ecological Monographs 11:191-227.

ANDREN, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794-804.

ARCESE, P., AND J. N. M. SMITH. 1988. Effects of population density and supplemental food on reproduction in song sparrows. Journal of Animal Ecology 57:119-136.

ASKINS, R. A., J. F. LYNCH, AND R. GREENBERG. 1990. Population declines in migratory birds in eastern North America. Current Ornithology 7: 1-57.

BARBA, E., D. M. GARCIA, J. A. GIL-DELGADO, AND G. M. LOPEZ. 1994. Moth abundance and breeding success in a great tit population where moths are the main nestling food. Ardea 82:329-334.

BOLLINGER, E. K., AND E. T. LINDER. 1994. Reproductive success of Neotropical migrants in a fragmented Illinois forest. Wilson Bulletin 106:46-54.

CAUGHLEY, G., AND A. GUNN. 1996. Conservation biology in theory and practice. Blackwell Science, Cambridge, Massachusetts, USA.

CRESSWELL, W. 1997. Nest predation: the relative effects of nest characteristics, clutch size and parental behaviour. Animal Behaviour 53: 93-103.

DARVEAU, M., G. GAUTHIER, J. L. DESGRANGES, AND Y. MAUFFETTE. 1993. Nesting success, nest sites, and parental care of the least flycatcher in declining maple forests. Canadian Journal of Zoology 71: 1592-1601.

DEGRAAF, R. M. 1995. Nest predation rates in managed and reserved extensive northern hardwood forests. Forest Ecology and Management 79:227-234.

DERLETH, E. L., D. G. MCAULEY, AND T. J. DWYER. 1989. Avian community response to small-scale habitat disturbance in Maine. Canadian Journal of Zoology 67:385-390.

DIAS, P.C., AND J. BLONDEL. 1996. Breeding time, food supply and fitness components of blue tits *Parus caeruleus* in Mediterranean habitats. Ibis 138:644-649.

DUGUAY, J. P. 1997. Influence of two-age and clearcut timber management practices on songbird abundance, nest success, and invertebrate biomass in West Virginia. Dissertation, West Virginia University, Morgantown, USA.

EHRLICH, P. R., D. S. DOBKIN, AND D. WHEYE. 1988. The birder's handbook. Simon & Schuster, New York, New York, USA.

FILLIATER, T. S., R. BREITWISCH, AND P. M. NEALEN. 1994. Predation on northern cardinal nests: does choice of nest site matter? Condor 96: 761-768.

GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871-883.

GREENBERG, C. H., AND A. MCGRANE. 1996. A comparison of relative abundance and biomass of ground-dwelling arthropods under different forest management practices. Forest Ecology and Management 89: 31-41.

GUNNARSSON, B. 1996. Bird predation and vegetation structure affecting spruce-living arthropods in a temperate forest. Journal of Animal Ecology 65:389-397.

HASKELL, D. G. 1995*a*. Forest fragmentation and nest predation: are experiments with Japanese quail eggs misleading? Auk 112: 767-770.

HASKELL, D. G. 1995*b*. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. Conservation Biology 9: 1316-1318.

HELLE, P., AND J. MUONA. 1985. Invertebrate numbers in edges between clear-fellings and mature forests in northern Finland. Silva Fennica 19:281-294.

HINES, J. E., AND J. R. SAUER. 1989. Program contrast. A general program for the analysis of several survival or recovery rate estimates. United States Fish and Wildlife Service, Technical Report 24, Washington, D.C., USA.

HOLMES, R. T., J.C. SCHULTZ, AND P. NOTHNAGLE. 1979. Bird predation on forest insects: an exclosure experiment. Science 206:462-463.

HOLMES, R. T., T. W. SHERRY, AND F. W. STURGES. 1991. Numerical and demographic responses of temperate forest birds to annual fluctuations in their food resources. ACTA XX Congressus Internationalis Ornithologici: 1559-1567.

HOLMES, R. T., P.P. MARRA, AND T.W. SHERRY. 1996. Habitat-specific demog-

raphy of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. Journal of Animal Ecology 65: 183–195.

HUTTO, R. L. 1985. Seasonal changes in the habitat distribution of transient insectivorous birds in southeastern Arizona: competition mediated? Auk 102: 120–132.

JOLIVET, P. 1986. Insects and plants: parallel evolution and adaptations. E. R. Brill-Flora and Fauna, New York, New York, USA.

LEIMGRUBER, P., W. J. MCSHEA, AND J. H. RAPPOLE. 1994. Predation on artificial nests in large forests blocks. Journal of Wildlife Management 58: 254–260.

MARQUIS, R. J., AND C. J. WHELAN. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology 75: 2007–2014.

MARTIN, T. E. 1986. Competition in breeding birds: on the importance of considering processes at the level of the individual. Current Ornithology 4: 181–210.

MARTIN, T. E. 1992. Interaction of nest predation and food limitation in reproductive strategies. Current Ornithology 9: 163–197.

MARTIN, T. E., AND G. R. GEUPEL. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64: 507–519.

MAYFIELD, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73: 255–261.

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87: 456–466.

MCGARIGAL, K., AND B. J. MARKS. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. United States Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-351, Portland, Oregon, USA.

MILLER, G. W., P. B. WOOD, AND J. V. NICHOLS. 1995. Two-age silviculture - an innovative tool for enhancing species diversity and vertical structure in Appalachian hardwoods. Pages 175–182 *in* L. G. Eskew. Forest health through silviculture. Proceedings of the 1995 National Silviculture Workshop. United States Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-GTR-267, 8–11 May 1995, Fort Collins, Colorado, USA.

NEWTON, I. 1980. The role of food in limiting bird numbers. Ardea 68: 11–30.

NICHOLS, J. V. 1996. Effects of two-age timber management and clearcutting on songbird density and reproductive success. Thesis, West Virginia University, Morgantown, USA.

NIEMELA, J. 1990. Spatial distribution of carabid beetles in the southern Finnish taiga: the question of scale. Pages 143–155 *in* N. E. Stork, editor. The role of ground beetles in ecological and environmental studies. Intercept, Andover, England.

NIEMELA, J., D. LANGOR, AND J. R. SPENCE. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Conservation Biology 7: 551–561.

OLIVER, C. D., AND B. C. LARSON. 1996. Forest stand dynamics. John Wiley and Sons, New York, New York, USA.

PRICE, T. 1985. Reproductive responses to varying food supply in a population of Darwin's finches: clutch size, growth rates and hatching synchrony. Oecologia 66: 411–416.

RODENHOUSE, N. L. 1986. Food limitation for forest passerines: effects of natural and experimental food reductions. Dissertation, Dartmouth College, Hanover, New Hampshire, USA.

RODENHOUSE, N. L., AND R. T. HOLMES. 1992. Results of experimental and natural food reductions for breeding black-throated blue warblers. Ecology 73: 357–372.

RODENHOUSE, N. L., L. B. BEST, R. J. O'CONNOR, AND E. K. BOLLINGER. 1995. Effects of agricultural practices and farmland structures. Pages 269–293 *in* T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University, New York, New York, USA.

SAMPLE, B. E., L. BUTLER, C. ZIVKOVICH, R. C. WHITMORE, AND R. REARDON. 1996. Effects of *Bacillus thuringiensis* Berliner var. *kurstaki* and defoliation by the gypsy moth [*Lymantria dispar* (L.) (Lepidoptera: Lymantriidae)] on native arthropods in West Virginia. Canadian Entomologist 128: 573–592.

SAS INSTITUTE. 1989. SAS User's Guide. SAS Institute, Cary, North Carolina.

SCHOWALTER, T. D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. Forest Ecology and Management 78: 115–125.

SCHOWALTER, T. D., J. W. WEBB, AND D. A. CROSSLEY, JR. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. Ecology 62: 1010–1019.

SMITH, H. C., N. I. LAMSON, AND G. W. MILLER. 1989. An esthetic alternative to clearcutting? Journal of Forestry 87: 14–18.

SULLIVAN, K. A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaenotus*). Journal of Animal Ecology 58: 275–286.

THOMPSON, F. R., III, W. D. DIJAK, T. G. KULOWIEC, AND D. A. HAMILTON. 1992. Breeding bird populations in Missouri Ozark forests with and without clearcutting. Journal of Wildlife Management 58: 23–30.

UNITED STATES FOREST SERVICE. 1986. Final environmental impact statement: land and resource management plan, Monongahela National Forest. United States Forest Service, Elkins, West Virginia, USA.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47: 893–901.

VICKERY, P. D., M. L. HUNTER, JR., AND J. V. WELLS. 1992. Is density an indicator of breeding success? Auk 109: 706–710.

WELSH, C. J. E., AND W. M. HEALY. 1993. Effect of even-aged timber management on bird species diversity and composition in northern hardwoods of New Hampshire. Wildlife Society Bulletin 21: 143–154.

WOLF, L., E. D. KETTERSON, AND V. NOLAN, JR. 1990. Behavioral response of female dark-eyed juncos to the experimental removal of their mates: implications for the evolution of male parental care. Animal Behaviour 39: 125–134.

YAHNER, R. H., AND A. L. WRIGHT. 1985. Depredation on artificial ground nests: effects of edge and plot age. Journal of Wildlife Management 49: 508–513.

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