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THE USE OF A FOREST CANOPY WALKWAY FOR STUDYING HABITAT SELECTION BY NEOTROPICAL MIGRANTS

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ABSTRACT. Birds are part of a three-dimensional matrix of interactions within the forest and often act as biological indicators of ecological stress. Because of the heights of temperate trees and the vertical complexities of forest ecosystems, however, our knowledge of bird ecology has been largely ground-based. Mist-netting provides useful data for forest conservation, but this census tool historically has ignored the use by migratory songbirds of woodland resources more than 3 meters above ground (the height of a typical mist-net). To examine stratification of neotropical migrants, this study uses a forest canopy walkway and aerial mist-nets (with ground replicates and other nets placed in nearby habitats) in New York State's Mid-Hudson Valley. The analysis is then related to forest conservation issues. Preliminary work shows stratification among some songbirds, especially when compared to a previous canopy mist-netting study in Massachusetts. Results suggest that these migrants play a valuable role in the biointegrity of temperate forest ecosystems.

Key words: neotropical migrants, resident birds, temperate forest canopy, strata utilization, biointegrity, aerial walkway, conservation

INTRODUCTION

Birds are integral parts of forest communities. Neotropical species collectively have been called "the world's largest vertebrate migration system" (Morton 1989). Breeding birds and certain winter residents are known to display a notable vertical partitioning of forest habitat (e.g., Chapman 1929, MacArthur 1958, Humphrey et al. 1968, Hecker 1991, Stokes & Schultz 1995). "Just as there is a marked stratification in the vegetation of the forest, so there is in the vertical distribution of forest birds" (Chapman 1929). Neotropical migrants utilize forest resources by predictable partitioning.

Birds such as the red-eyed vireo and northern parula forage primarily in the canopy, whereas the wood thrush and ovenbird frequent the understory. Still other species, such as the black-throated blue warbler and the white-breasted nuthatch, are found in both strata. Few attempts have been made to quantify the vertical distribution of neotropical migrants in northern temperate forests because of access difficulties, expense, and a belief that ground-based observers can census canopy birds accurately. Waide and Narins (1988), in their study of tropical birds in Puerto Rico, conducted simultaneous variable circular-plot censuses. They concluded that "Canopy foliage density seems to be effective in attenuating sound from the canopy to the ground, as well as from the ground to the canopy. The former is important for ground-based observers because it results in the bias against canopy-singing species." In addition, the dense foliage of northern temperate forests during the spring and summer is a confounding factor for accurate sampling in this ecosystem type and necessitates access for canopy censuses.

Strata utilization by birds becomes a pressing topic for forest conservation efforts. Many researchers have pointed out that neotropical migrants reflect the regional health of the environment, because they can interconnect environmental conditions in one area with another thousands of km away (e.g., see Rappole et al. 1983, Marra et al. 1998, and Sillett et al. 2000). Migratory songbirds thus can be used as a kind of litmus test for the overall soundness of ecological regions. For decades, attention focused on the complex horizontal components of forest habitat usage, including geographical distribution of species, fragmentation effects, and invasion of exotics. The equally heterogeneous vertical elements were addressed less rigorously.

Niches used by forest birds occupy a three-dimensional matrix in the ecosystem. Since wildlife management decisions sometimes are made with data obtained from mist-net sampling (Stokes 1997), analysis of the entire avian community is indispensable for forest conservation. Because of the multiple forest habitats involved with migratory bird species, the biointegrity (or ecological soundness) of large-scale regions may now depend on a more comprehensive approach to forest management.

Because of the heights of temperate trees and the vertical complexities of forest ecosystems, knowledge of canopy bird ecology remains rudimentary. Recent developments of reliable canopy-access systems, however, make the treetops safely accessible to nearly everyone interested in bird conservation (see Rinker 2000, 2001). For the first time in the history of bird-banding, researchers have protocols and equipment available to study the use by songbirds of all forest strata.

Since the early 1990s, a defining decade for canopy research, more than 100 field sites have been established worldwide for canopy science, with a majority focused on insects and plants (see Lowman & Wittman 1996). Few concentrate on birds. The only pertinent study in the 1990s on stratification of migrating songbirds was a collaborative project conducted by researchers at Hampshire College and the University of Massachusetts in Amherst (Stokes 1997). Researchers simultaneously netted birds in the canopy and understory strata of a mature deciduous forest patch in western Massachusetts during three migration seasons (fall 1994, spring and fall 1995) using the forest canopy walkway at Hampshire College. As a short-term project, the Hampshire College study could offer no comparative data from similar banding stations.

Using a newly constructed forest canopy walkway and an established bird-banding program at Millbrook School, I documented habitat selection among neotropical migrants in a mature oak-maple forest in New York State's Mid-Hudson Valley during four migratory seasons (spring and fall, 1997 and 1998). This paper compares results of the Millbrook School study with those of the Hampshire College study and discusses implications of songbird stratification for forest management and conservation. Since few researchers have worked long-term with canopy avifauna, the Millbrook study proposed to answer two related questions:

1. Do neotropical migrants stratify at the Millbrook School forest canopy walkway in a way similar to that noted by researchers at other temperate sites?
2. Do capture rates differ between resident and migratory species?

During the launching of the Millbrook School study, other questions emerged; they are listed in the conclusion as a future direction for canopy ornithology.

Materials and Methods

In late spring 1995, Millbrook School constructed a canopy walkway (41°51′N, 73°37′W) on the south end of the 240-ha campus in an 80-ha mixed woods. Four healthy, full-sized red oaks (*Quercus rubra*), each with an upper canopy reaching ca. 26 m, support the walkway and give access to the upper story of the surrounding forest. The trees grow on a southeast-facing wooded hillside with a 30° slope, good drainage, and loamy-textured soil with a pH between four and five. Site elevation is 280 m above sea level. Predominant hardwood vegetation at the site includes red oak, sugar maple (*Acer saccharum*), cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), and white oak (*Quercus alba*). Noteworthy herbaceous flora include wood fern (*Dryopteris* sp.), hayscented fern (*Dennstaedtia punctilobula*), blood root (*Sanguinaria canadensis*), trout lily (*Erythronium americanum*), and jack-in-the-pulpit (*Arisaema* sp.).

Common spring birds on the hillside include the wood thrush, veery, scarlet tanager, pileated woodpecker, red-bellied woodpecker, downy and hairy woodpeckers, eastern wood pewee, gray catbird, rufous-sided towhee, yellow warbler, blue jay, yellow-billed cuckoo, and common nighthawk. Red-tailed hawks and great horned owls nest in the surrounding forest. Ten of these species are listed in Table 1.

The walkway consists of four research platforms 15 to 20 m in height and three connecting bridges with a 35 m total span through the treetops. It is a Y-shaped modular system developed by Canopy Construction Associates in Amherst, Massachusetts (see Lowman & Bouricius 1995). The bridges are made of grooved wooden ties bolted to stainless steel connectors. The platforms consist of wood timbers supported by wire cables, with cable handrails and safety webbing located appropriately (see Figures 1 and 2 for architectural details). Weather data are logged hourly in the canopy and on the ground for temperature, relative humidity, wind speed and direction, solar radiation in the 400–700 nm photosynthetic range, and precipitation (see Table 2, note 2). Throughout the migratory seasons, insects are captured via standard malaise traps on the ground and in the canopy to sample possible food sources for songbirds.

From 1939 to 2000, the school operated a student-training program in bird banding and held a master station permit for banding from the U.S. Fish and Wildlife Service and the New York State Department of Environmental Conservation. More than 25,000 birds were banded during those 60+ years, representing ca. 100 species. From spring 1997 to spring 2000, the school's banding program was based entirely at the forest canopy walkway.

The technique for deploying mist-nets in the forest canopy was piloted by Stokes and Schultz (1995), using the Hampshire College walkway in a 6-ha forest fragment in central Massachusetts. To study neotropical migrants through three consecutive seasons, Stokes and Schultz

TABLE 1. Overall capture rates at net locations in various habitats for the Millbrook School Forest Canopy Walkway (three canopy nets, three floor replicates, two edge nets, and two hedgerow nets). The first number for species refers to spring captures, the second to fall.

Species	Canopy	Floor	Edge	Hedgerow
RESIDENTS (R)				
Blue jay (*Cyanocitta cristata*)	0/0	1/1	0/0	0/0
Brown creeper (*Certhia americana*)	0/1	0/1	0/0	0/0
Downy woodpecker (*Picoides pubescens*)	0/0	1/1	0/0	0/0
Tufted titmouse (*Parus bicolor*)	1/0	3/2	0/0	0/0
Hairy woodpecker (*Picoides villosus*)	2/0	1/0	0/0	0/0
Red-bellied woodpecker (*Melanerpes carolinus*)	1/1	0/0	0/0	0/0
White-breasted nuthatch (*Sitta carolinensis*)	2/1	1/2	0/0	0/0
Total individuals	*6/3*	*7/7*	*0/0*	*0/0*
Total net-hours (n-h)	*427.25*	*578.45*	*127.95*	*234.0*
Capture rate (# inds/100 n-h)	*1.40/0.70*	*1.21/1.21*	*0.00/0.00*	*0.00/0.00*
Overall capture rate (# inds/100 n-h)	*2.11*	*2.42*	*0.00*	*0.00*
MIGRANTS (M)				
American robin (*Turdus migratorius*)	0/2	3/10	2/9	6/10
American goldfinch (*Carduelis tristis*)	0/0	1/0	0/0	0/0
Brown-headed cowbird (*Molothrus ater*)	3/0	0/0	0/0	0/0
Black-and-white warbler (*Mniotilta varia*)	0/2	0/0	0/0	0/0
Blackpoll warbler (*Dendroica striata*)	0/1	0/0	0/0	0/0
Black-throated blue warbler (*D. caerulescens*)	1/0	0/1	0/0	0/0
Black-throated green warbler (*D. virens*)	1/1	0/0	0/0	0/0
Blue-winged warbler (*Vermivora pinus*)	1/0	0/0	0/0	0/0
Chipping sparrow (*Spizella passerina*)	0/0	0/0	0/0	0/1
Eastern phoebe (*Sayornis phoebe*)	0/0	2/0	0/0	1/2
Eastern wood-pewee (*Contopus virens*)	1/0	0/0	0/0	0/0
Field sparrow (*Spizella pusilla*)	0/0	0/0	0/0	2/0
Fox sparrow (*Passerella iliaca*)	0/0	0/0	0/0	0/2
Gray catbird (*Dumetella carolinensis*)	1/0	1/0	3/0	3/1
House wren (*Troglodytes aedon*)	0/0	0/0	0/0	0/1
Indigo bunting (*Passerina cyanea*)	0/0	1/0	1/0	0/0
Myrtle warbler (*Dendroica coronata*)	1/0	0/0	0/0	0/0
Ovenbird (*Seiurus aurocapillus*)	0/0	1/0	0/0	0/0
Red-eyed vireo (*Vireo olivaceus*)	0/0	1/0	0/0	0/0
Red-winged blackbird (*Agelaius phoeniceus*)	0/0	0/0	2/0	2/0
Rose-breasted grosbeak (*Pheucticus ludovicianus*)	1/0	0/0	0/0	0/0
Ruby-crowned kinglet (*Regulus calendula*)	0/0	0/0	1/0	0/0
Scarlet tanager (*Piranga olivacea*)	2/1	4/0	0/0	0/0
Song sparrow (*Melospiza melodia*)	0/0	0/0	1/0	3/1
Veery (*Catharus fuscescens*)	0/0	4/0	0/0	2/0
Wood thrush (*Hylocichla mustelina*)	0/0	4/0	0/0	0/0
White-throated sparrow (*Zonotrichia albicollis*)	0/0	0/0	0/0	1/3
Yellow palm warbler (*Dendroica palmarum*)	0/0	0/0	2/0	0/0
Yellow warbler (*D. petechia*)	0/0	0/0	1/0	1/0
Total individuals (inds)	*12/7*	*22/11*	*13/9*	*21/21*
Total net-hours (n-h)	*427.25*	*578.45*	*127.95*	*234.0*
Capture rate (# inds/100 n-h)	*2.81/1.64*	*3.80/1.90*	*10.16/7.03*	*8.97/8.97*
Overall capture rate (# inds/100 n-h)	*4.45*	*5.70*	*17.19*	*17.95*
Habitat capture rate (R + M)	***4.21/2.34***	***5.01/3.11***	***10.16/7.03***	***8.97/8.97***
Overall habitat capture rate (R + M)	***6.55***	***8.13***	***17.19***	***17.95***

suspended three standard 12-m nets (with 36-mm mesh openings) near a canopy platform 22 m in height. They placed replicate nets on the ground directly under those in the treetops, and birds were retrieved from the upper set by way of a drapery system attached to a clothesline pulley. Spindles at the platform end of the nets allowed workers to wrap and unwrap nets to reach the captured birds, as the nets slid to and from the platform.

The Millbrook School setup was constructed similarly (FIGURE 3), except that we deployed 10 nets with a smaller mesh (30-mm) to avoid the warbler escapes frequently noted at Hampshire

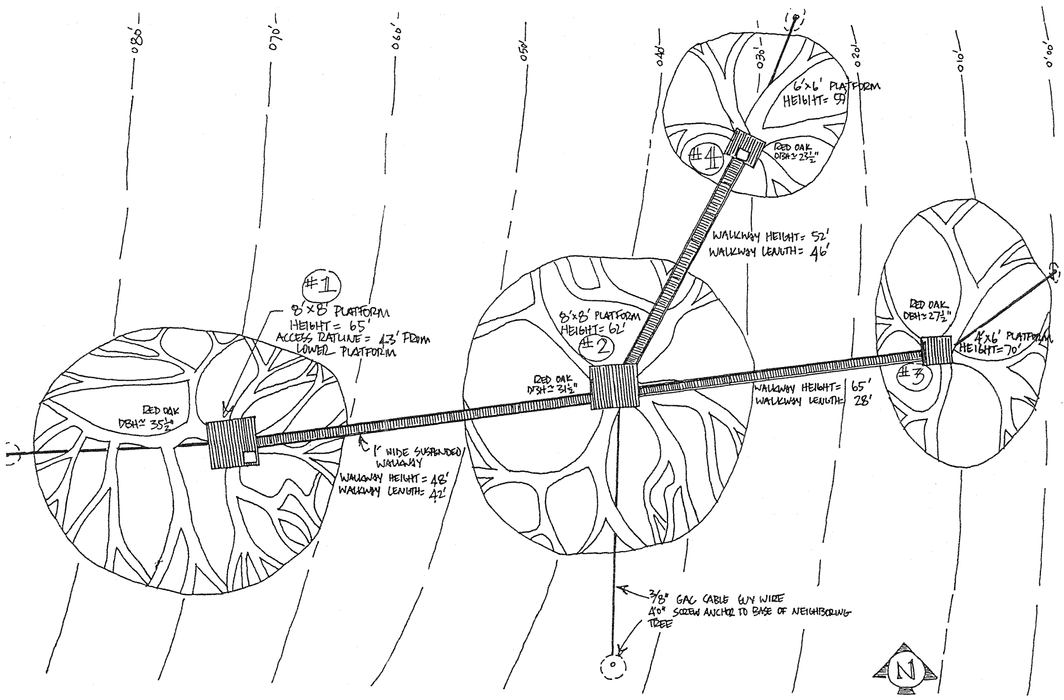

FIGURE 1. Aerial perspective of the Millbrook School Forest Canopy Walkway. All drawings are based on the isometric renderings by Eric Kaye Designs for Canopy Construction Associates (Amherst, Massachusetts) and are not to-scale.

(Stokes, pers. comm.). Three nets extended from two canopy platforms, three were placed on the ground as replicates (0.5–3.0 m from the floor), and the other four were stationed elsewhere on the forest floor and in nearby fields for comparative ecological sampling. Canopy Construction Associates again was contracted to place suitable hardware in the appropriate trees adjacent to the research platforms. Student and adult volunteers manned the banding station from 30 min. after sunrise to midmorning through the spring and fall migrations annually. Set-up time was approximately 45 min. including the time needed to climb to the research platforms. Nets were checked at 20-min. intervals. Volunteers remained stationed whenever possible at each set of nets to record bounce-outs. Birds were removed from the nets and delivered to our ground banding station at the base of the primary climbing tree. Canopy birds were bagged and lowered directly to the station via a clothesline pulley system.

PRELIMINARY RESULTS AND DISCUSSION

After four consecutive migration seasons (spring and fall, 1997 and 1998), we accumulated more than 1300 net-hours where 1 n-h = 1 hour of operation for each 2.5 × 12-m net. Volunteers banded 139 birds representing 36 species. We captured 28 birds (20%) in the three canopy nets, 47 birds (34%) in three ground replicates, and 64 birds (46%) in the other four sampling nets. All 10 nets were active, although the five most productive (in descending order) were a hedgerow net, a forest edge net, a forest floor net, another hedgerow net, and a canopy net. Capture rates are given in TABLE 1. Species are grouped according to their resident or migratory status and according to capture-habitat (i.e., forest canopy, forest floor, forest edge, and hedgerow).

Our initial results make an interesting comparison to the findings of Stokes and Schultz (see TABLE 3), especially when spring data are separated from fall data. Out of 36 species recorded at the Millbrook site, eight were captured in both canopy and ground nets (not including those along the forest edge and hedgerows). Nine were netted exclusively in the canopy, and nine were found only on the forest floor. Notably, all warblers except for the black-throated blue warbler, the ovenbird, the yellow palm warbler, and the yellow warbler were captured in the canopy nets—-predicted by their known foraging habits and by previous stratification studies.

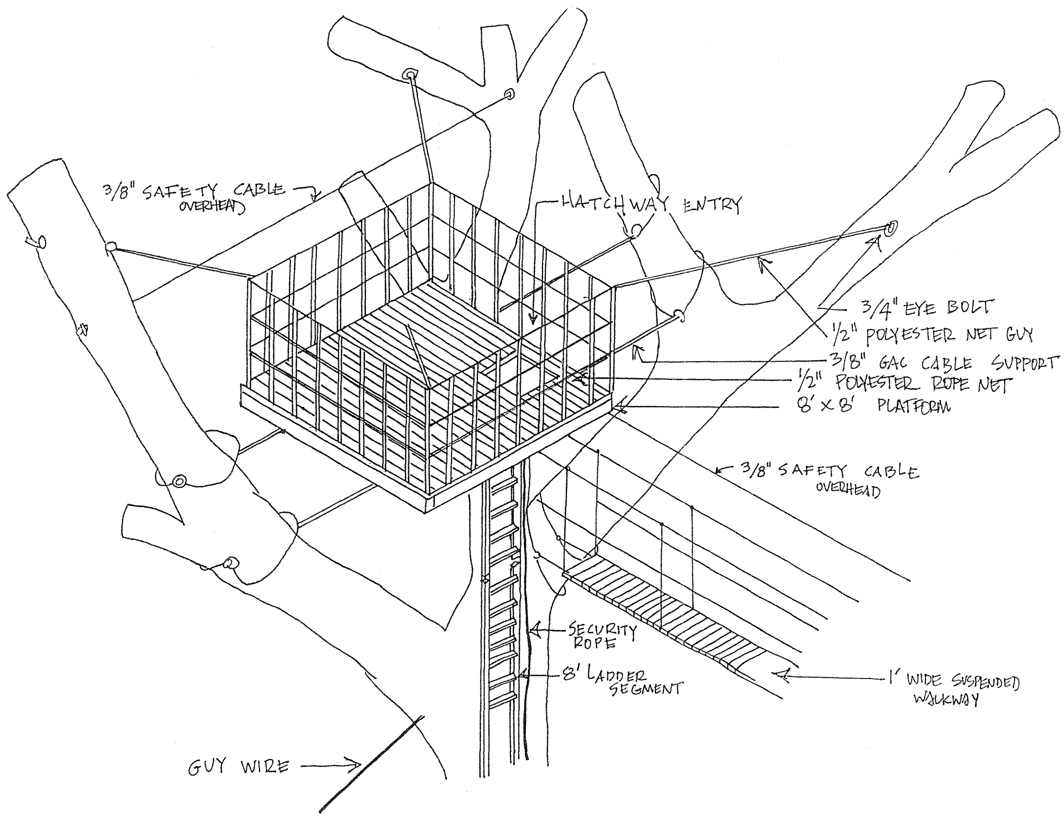

FIGURE 2. Isometric design of the research platforms for the Millbrook School Forest Canopy Walkway.

Two species typically viewed as upper canopy or field-loving birds (red-eyed vireo and indigo bunting, respectively) were netted on the ground. Pairs (never singles) of scarlet tanagers were caught in both ground and treetop nets, although one individual did escape. Thus, 35% of the total capture to-date were exclusively canopy species, 35% exclusively ground species, and 31% were found in both strata. The Hampshire College study found 45%, 41%, and 14%, respectively (Stokes 1997).

Migrants comprised approximately 83% (116 individuals) of total captures while residents made up 17% (23 individuals). Differentiating total captures into spring and fall samples, similar proportions were found: Spring migrants (84%) and residents (16%) versus fall migrants (83%) and residents (17%). When only canopy and replicate ground nets were considered (minus net captures for the forest edge and hedgerows), the results closely resembled those of Stokes (1997). Migrants comprised 69% (52 individuals) of total captures at Millbrook, while residents made up 31% (23 individuals). Breaking total captures into spring and fall samples gave similar proportions of migrants and residents: 72% and 28% for the spring, respectively, and 64% and 36% for the fall, respectively.

Stokes (1997) captured 40 species at the Hampshire College station during three consecutive migrations, while the Millbrook station caught 36 species during four seasons. The total net-hours varied considerably with the availability of volunteers (more than 1000 n-h at Millbrook for the canopy and ground-replicate nets to slightly more than 5000 n-h at Hampshire). Lower volunteer hours may account for lower numbers for all categories at the New York site. Stokes also noted that the Hampshire College station captured more canopy birds than ground birds during the fall migration, but the reverse was true for the spring season. He attributed this seasonal shift to a number of possible reasons, including fall recruitment of hatch-year birds, inadequate sampling of foliage gleaners in the canopy, high visibility of mist-nets during the early spring, and high escape rates of canopy guild species as a result of the large mesh size (36 mm) of his nets. Overall, however, the

TABLE 2. Budget for canopy access structure at Millbrook School based on approximate 1995 costs.

Budget items	1995 costs
Canopy walkway[1]	
Materials	$9100.00
Labor	8400.00
Ground platform	
Materials	400.00
Labor	600.00
Weather station[2]	
Materials	6500.00
Labor	500.00
Canopy mist-netting[3]	
Materials	1500.00
Labor	2500.00
Climbing gear for four persons[4]	600.00
Total	$30,100.00

[1] Includes four study platforms, three bridges, and one access ladder.

[2] Weather instrumentation includes a Scientific Sales Model 8120 large instrument shelter, a Campbell Scientific 21 XL micrologger with supporting interfaces and software, an MSX10 10-watt solar panel, and ENC 12/14 environmental enclosure for the datalogger, two Li-Cor LI190SB-L quantum sensors (400–700 nm), two Vaisala Model HMP35C temperature and relative humidity probes, a Campbell Scientific Model 41002 solar radiation shield for one temp/RH probe, two Met-One Model 024A wind direction sensors, and two Met-One 014A 3-cup anemometers. One set of instruments is located on the ground in the instrument shelter along with the datalogger, and a second is positioned in the canopy approximately 20 m over the shelter.

[3] Materials include three canopy nets and seven ground nets with supporting hardware. Labor included consulting fees, costs of initial training and supervising of volunteers, and canopy branch removal for the upper net lanes.

[4] The system permits a maximum of four people on it at any one time, including the primary instructor. Each must follow an established access protocol at all times, including the use of technical climbing gear. The equipment includes four ascenders for use as safety devices while climbing, four helmets, four harnesses, four double safety lanyards, and eight auto-locking carabiners.

Hampshire College station collected more birds on the ground than in the canopy.

The Millbrook station also captured more birds on the ground than in the canopy. We noted that our spring captures showed a similar vertical difference: more activity on the ground than in the treetops. Unlike the Hampshire site, however, that difference was also true for our fall captures. Another dissimilarity between the Millbrook and Hampshire stations can be seen when the spring and fall migration seasons are separated for numbers of birds captured per 100 net-hours. Whether canopy or floor captures are compared, the spring data are more than four times higher than those from the fall. These differences may result from the flow of migratory species over the site (i.e., birds sweeping northward may follow the slope of the forest more closely than birds passing over the same forested hillside on their way southward). The flyways for neotropical migrants may vary greatly between spring and fall. The timing of our captures may have had an effect on the data: we banded only from sunrise to midmorning. Insects, too, may be a greater attraction for their avian predators during the spring than they are later in the year. Outbreaks (e.g., lepidopteran larvae) are more common on young leaves in the spring than in the fall when leaves have accumulated higher concentrations of secondary compounds. Data on arthropod abundance from canopy and ground malaise traps are still being processed. During the fall, the nets may become more visible to birds as leaves are dropped.

CONCLUSION

Few conclusions can be drawn from only four seasons of operation and from so few data. Limitations include a single banding station with only 10 sampling nets, a cadre of adult and student volunteers with varying schedules and bird-identification skills, and placement of two of the three canopy nets at 90° to the contour, thus sampling various forest strata concurrently. Despite these limitations, this study addresses some of the inherent biases in ground-based netting by sampling canopy and ground migrants simultaneously. The Millbrook project also allowed comparison of forest data with other ecological types of vegetation.

Stokes (1997) stated in his study that "conventionally-placed mist nets undersampled the canopy foraging guild . . . ." Observers at both the Massachusetts and New York sites frequently noted species of foraging migrants present in the forest fragments that were never captured in mist-nets (see Rinker 2001). Based on our work at the Millbrook School site, we agree with Stokes that the canopy guild is undersampled by ground-based netting during migration. These birds are even undersampled by current protocols for mist-netting in the canopy. Migrants stratify vertically in forests and do not shift between forest strata from season to season. Many are insectivorous foliage gleaners adapted to life in the treetops. Ground-based netting then yields information about ground-based birds and little or nothing about songbirds in the upper strata of forests. Both the Hampshire College and the

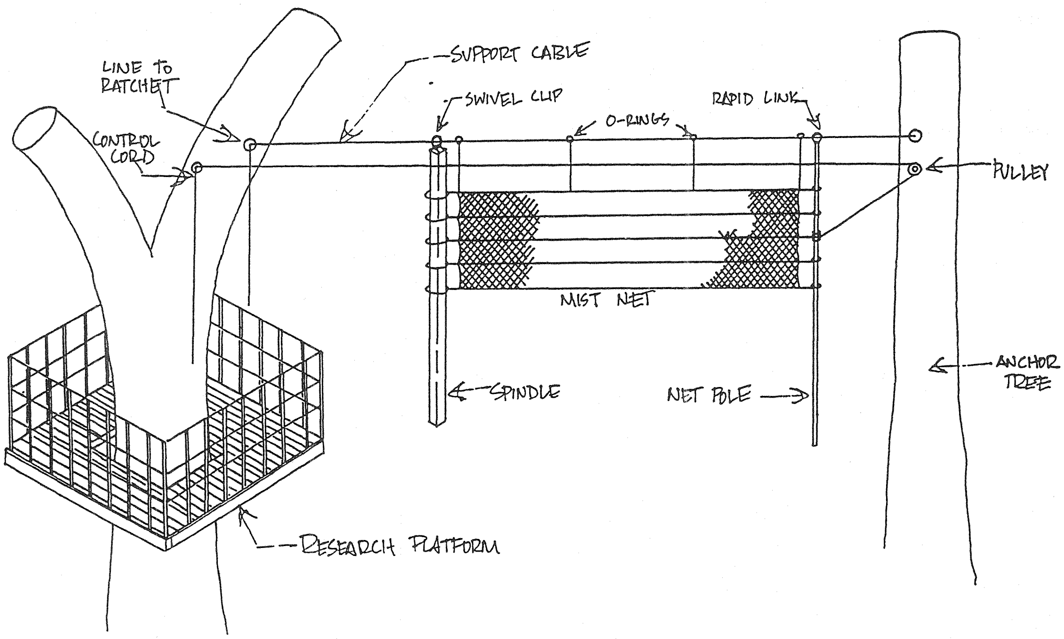

FIGURE 3. Construction design of the canopy mist-nets for the Millbrook School Forest Canopy Walkway. Drawing is adapted from Stokes and Schultz (1995) and Stokes (1997).

Millbrook School pilot studies clearly call for more intensive banding in all layers of forest vegetation.

Birds traditionally have been viewed as biological indicators of environmental health. Few banding stations in North America have been committed to working long-term in the treetops. Thus, the resulting picture from our national banding efforts is an incomplete one, especially for issues of forest management. A coordinated effort among existing North American walkways and other canopy access systems is needed for a comprehensive view of the avifaunal forest mosaic. We encourage schools, universities and colleges, local and regional park authorities, and private landowners with forest preserves to consider the construction of canopy walkways for licensed bird studies. Although expensive and energy-intensive, banding programs from forest canopy walkways can offset some of the biases of population sampling from the ground. "For canopy research of birds to advance and address . . . fundamental ecological questions and conservation concerns, it is essential that more intensive netting and marking of canopy birds of all sizes be undertaken" (Munn & Loiselle 1995).

Long-term, coordinated banding programs in

TABLE 3. Comparison of data for both the Millbrook School (Millbrook, New York) and Hampshire College (Amherst, Massachusetts) sites. Data for the Millbrook station includes captures only in the canopy and replicate ground sites.

Captures	No. individuals Canopy/floor	No. inds/100 n-h Canopy/floor	No. species Canopy/floor/both	Total n-h Canopy/floor
Millbrook School[1]	30/48	6.55/8.13	9/9/8	427.25/578.45
Spring 1997 and 1998	18/30	15.52/18.55	8/9/5	116.00/161.70
Fall 1997 and 1998	12/18	3.86/4.32	5/3/3	311.25/416.75
Hampshire College[2]	121/159	6.9/4.7	25/23/8	1751/3386
Spring 1995	21/90	3.8/8.1	10/17/3	559/1117
Fall 1994	35/18	7.6/2.3	16/9/3	451/786
Fall 1995	65/51	8.8/3.4	15/16/4	741/1483

[1] Data from four seasons (spring and fall, 1997 and 1998).
[2] Data from three seasons (fall 1994, spring 1995, and fall 1995).

the treetops of North America and beyond can help to provide a clearer picture of strata utilization than that acquired through ground-based netting alone. Such programs can focus on a number of questions that emerged from this study. Do certain species (e.g., warblers) distinguish between a tree canopy and the canopy of a field? Do nets in a field along migration routes compare quantitatively to those in the forest? Immediately north of the forest fragment that contains the canopy walkway in this study are several large fields surrounded by hedgerows. Do canopy birds "jump" over these to the next forest or do the birds also glean insects from the tops of grasslands as they migrate? Is avifaunal stratification connected to forest microclimate (viz., canopy vs. ground)? Do correlations exist between insect abundance and bird stratification? Is analysis of the Millbrook data applicable to forest conservation issues (e.g., forest fragmentation, mixed-aged stands, canopy heterogeneity, keystone species)? How important are hedgerows and forest edges to migrating birds? Because the Millbrook forest fragment is 13 to 14 times larger than that used by Stokes and Schultz (1995), will the Millbrook capture rates increase accordingly? If so, does the MacArthur and Wilson model for ecological insularity (1967) apply to these studies? What are the long-term effects of aerial walkways on supporting and surrounding vegetation and wildlife populations? Understanding the three-dimensional matrix of bird activity in our forests, undoubtedly, will provide clues about the biointegrity of this complex natural resource.

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