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DANIEL L. COMBS AND LEIGH H. FREDRICKSON, *School of Natural Resources, Univ. of Missouri–Columbia, Gaylord Memorial Laboratory, Puxico, Missouri 63960* (Present address DLC: *Department of Biology, Tennessee Technological University, Cookeville, Tennessee 38505*). Received 10 June 1994, accepted 1 Dec. 1994.

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Habitat use by wintering and breeding bird communities in relation to edge in an irrigated forest.—About 1% of the 2000 municipal sewage systems in the United States that apply wastewater to terrestrial habitats apply it to forested landscapes (W. E. Sopper, pers. commun.; Urie 1986). This is expected to increase as small, localized sewage systems are needed in nonagricultural areas (Nutter and Red 1986). Wastewater application changes structure and species composition of forest understory plants, distribution of fruit-producing plants, and abundance of invertebrates on the forest floor (Sopper and Kardos 1973, Lewis 1977, Mastrota et al. 1989, Rollfinke and Yahner 1990). Wastewater application also has been found to affect abundance and distribution of avian species, particularly those that forage and nest near ground level (e.g., Lewis and Sampson 1981, Rollfinke and Yahner 1990, Rollfinke et al. 1990). These avian studies, however, were relatively restricted in area or were based on mist-netting data collected only during the breeding season. Furthermore, establishment and maintenance of a wastewater-application system produces a considerable amount of edge habitat because of the network of irrigation pipes and access roads. In this study, my objective was to determine use of four habitat types by wintering and breeding bird communities in relation to distance from an edge from 1987–1991 in a forest-farmland landscape, part of which was affected by wastewater irrigation in central Pennsylvania.

Study area and methods.—I conducted the study on State Game Lands 176 in Centre County, Pennsylvania, from 1987–1991 (see details in Rollfinke and Yahner 1990, Rollfinke

et al. 1990). The irrigated sector of the study area contained a 200-ha wastewater-irrigation system that began operation in 1983. The system consisted of about 3100 rotating sprinklers along a network of lateral pipes, which pumped an average of 264 cm of wastewater annually during the study; this was about three-fold the normal annual precipitation (93 cm) in central Pennsylvania (Matula 1983). Wastewater sprayed from sprinklers reached a height of about 4 m and a radius of 10–15 m from each sprinkler nozzle; nozzles were spaced 26 m apart. The irrigated sector consisted of an intermix of approximately 50% forest and 50% farmland and was traversed by numerous unimproved access roads. The non-irrigated sector used in my study was forested and adjacent to the irrigated sector.

Maximum age of overstory trees (woody stems ≥ 1.5 m tall, >7.5 cm dbh) in both the irrigated and the non-irrigated sectors was about 65–70 years old. Principal overstory trees in both sectors were quaking aspen (*Populus tremuloides*), bigtooth aspen (*P. grandidentata*), scarlet oak (*Quercus coccinea*), black oak (*Q. velutina*), northern red oak (*Q. rubra*), red maple (*Acer rubrum*), and pitch pine (*Pinus rigida*). Densities (no./ha) and basal areas (m^2/ha) of overstory trees were greater in the irrigated than in the non-irrigated sector (see details of vegetation in Rollfinke and Yahner 1990, Rollfinke et al. 1990), probably because wastewater irrigation promotes higher rates of tree growth (Sopper and Kardos 1973). Major understory trees (2.5–7.5 cm dbh) and shrubs (<2.5 cm in diameter) in both sectors were quaking aspen, red maple, rose (*Rosa* spp.), and Tartarian honeysuckle (*Lonicera tatarica*). Because of winter ice buildup from wastewater and subsequent stem breakage on understory trees and shrubs, understory trees and shrubs were about four-fold and three-fold less abundant on the irrigated than on the non-irrigated sector, respectively. Herbaceous ground cover was 57% on the irrigated sector compared with 5% on the non-irrigated sector. Ground cover on the irrigated sector was predominantly white snakeroot (*Eupatorium rugosum*), common pokeberry (*Phytolacca americana*), and Canada clearweed (*Pilea pumila*), which formed a lush layer of vegetation at least 2 m in height in some places. These differences in vegetation between the irrigated and the non-irrigated sectors did not exist prior to application of wastewater (Sopper and Kardos 1973).

A 100×100 -m grid was superimposed on a map of the study area. Thirty permanent sampling points were selected randomly in forested habitat and were divided into four habitat types; types 1–3 were in the irrigated sector and type 4 was in the non-irrigated sector. Sampling points in type-1 habitat ($N = 4$) contained only deciduous overstory trees and were 15–40 m from an edge, points in type-2 habitat ($N = 6$) had a mix of deciduous and coniferous overstory trees and were 60–125 m from an edge, points in type-3 habitat ($N = 14$) contained only deciduous overstory trees and were 60–125 m from an edge, and points in type-4 habitat ($N = 6$) were reference sites with deciduous overstory trees and were 75–150 m from an edge. Sampling points in type-1, type-3, and type-4 habitats contained less than 3% coniferous overstory trees (pitch pine or white pine [*Pinus strobus*]) versus approximately 28% coniferous overstory trees in type-2 habitat (R. H. Yahner, unpubl. data). The number of points per habitat type in the irrigated sector was selected on the basis of the approximate availability of forested habitat with a given cover type and distance to an edge. An edge was defined as the interface between wooded habitat containing overstory trees and a non-wooded disturbed area (crop field, old field, or unimproved dirt road) (after Forman and Godron 1986, Yahner 1988).

The 30 points were visited six times per season from Late December to early March during two winters (1988–1989 and 1990–1991) and from late May to early July during three breeding seasons (1987, 1989, and 1991). Visits occurred between sunrise and 10:00 h, and the order of visits was randomized. At each visit, an initial 1-min equilibrium period was followed by a 5-min observation period. All birds seen or heard within a 30-m radius of the center of the point during the 5-min period were counted (DeSante 1986, Morrison

TABLE 1

TOTAL NUMBER OF CONTACTS PER FORAGING BUILD IN AN IRRIGATED AND A NON-IRRIGATED SECTOR OF A STUDY AREA ON STATE GAME LANDS 176 DURING TWO WINTERS AND THREE BREEDING SEASONS IN CENTRAL PENNSYLVANIA, 1987-1991

Foraging guild	Winter			Breeding			
	1988-1989	1989-1990	Total	1987	1989	1991	Total
Ground-shrub forager	111	91	202	209	161	324	694
Trunk-bark forager	59	67	126	26	13	21	60
Sallier-canopy forager	0	4	4	228	98	165	431

et al. 1986, Yahner 1993). The total number of contacts obtained during the six visits was pooled for each point by season ($N =$ five, two winters and three breeding seasons) for each foraging guild (ground-shrub, trunk-bark, and sallier-canopy forager) or species (guild classifications followed those of Yahner 1986, 1993).

The total number of contacts per guild or common species (defined as a species with >20 contacts in a given season or seasons combined) was compared among the four habitat types for each of the five seasons separately, both winters combined, and the three breeding seasons combined, using G -tests for goodness-of-fit (Sokal and Rohlf 1981). The expected number of contacts was obtained by multiplying the proportion of total permanent sampling points per habitat type by the total number of contacts per guild or common species in a given season(s). Data were pooled between winters and among breeding seasons to give an additional measure of habitat-use patterns among habitat types and to increase sample size for statistical analyses (Rice et al. 1984, Yahner 1986). When a statistical difference in the number of contacts of a guild or a common species occurred among the four habitat types in a given season(s), a posteriori G -tests for goodness-of-fit were conducted about the cell (habitat type) of interest (Sokal and Rohlf 1981). Statistical differences were designated as $P < 0.05$ for all analyses.

Results.—Most contacts of wintering birds were those of ground-shrub (60.8%) and trunk-bark foragers (38.0%) (Table 1). Twenty-five bird species were observed on the study area in winters 1988-1989 and 1990-1991 combined, and approximately one-third (32.0%) of these were common species. The five most abundant species in order of decreasing total number of contacts were three trunk-bark foragers, Black-capped Chickadee (*Parus atricapillus*), Tufted Titmouse (*P. bicolor*), and Downy Woodpecker (*Picoides pubescens*) and two ground-shrub foragers, Dark-eyed Junco (*Junco hyemalis*) and White-throated Sparrow (*Zonotrichia albicollis*).

Type-1 habitat was used more than expected by ground-shrub foraging species in winter (Table 2). Species occurring more than expected in this habitat included Dark-eyed Junco, Northern Cardinal (*Cardinalis cardinalis*), and White-throated Sparrow. Type-2 habitat was used principally by trunk-bark foragers, e.g., Black-capped Chickadee, Tufted Titmouse, and Downy Woodpecker. Type-3 habitat was used in proportion to its availability in winter but tended to be preferred by Dark-eyed Juncos. Type-4 habitat was used less than expected by the wintering bird community, especially by four common species: Tufted Titmouse, Dark-eyed Junco, Northern Cardinal, and White-throated Sparrow.

More than twice as many species ($N = 54$) were noted on the study area in the breeding seasons during 1987, 1989, and 1991 combined as compared with winter seasons. As in winter, the major foraging guild in the breeding seasons was ground-shrub foragers (58.6%

TABLE 2

TOTAL NUMBER OF CONTACTS PER FORAGING GUILD IN FOUR HABITAT TYPES BY SEASON(S) IN AN IRRIGATED AND A NON-IRRIGATED SECTOR OF A STUDY AREA ON STATE GAME LANDS 176 IN CENTRAL PENNSYLVANIA, 1987–1991

Foraging guild ^a	Season	Habitat type			
		I	II	III	IV
Ground-shrub foragers	Winter 1988–1989	35 ^b	19	46	11 ^c
	Winter 1990–1991	22 ^b	26	35	8 ^c
	Both winters	57 ^b	45	81	19 ^c
	Breeding 1987	58 ^b	32	83 ^c	36 ^c
	Breeding 1989	49 ^b	33	55 ^c	24
	Breeding 1991	69 ^b	69	156	30 ^c
	All breeding	176 ^b	134	294 ^c	90 ^c
Trunk-bark foragers	Winter 1988–1989	10	23 ^b	21	5 ^c
	Winter 1990–1991	6	24 ^b	27	10
	Both winters	16	47 ^b	48	15
Sallier-canopy foragers	Breeding 1987	79 ^b	28 ^c	82 ^c	39
	Breeding 1991	14	31	101 ^b	19 ^c
	All breeding	40 ^c	83	234 ^c	74

^a Only guilds with a significant ($G \geq 7.82$, $df = 3$, $P < 0.05$) difference in number of contacts among habitat types in a given season(s) are given in the table.

^b Number of contacts was significantly ($G > 3.84$, $df = 1$, $P < 0.05$) greater in this habitat type than in the other three types combined.

^c Number of contacts was significantly ($G > 3.84$, $df = 1$, $P < 0.05$) less in this habitat type than in the other three types combined.

of total contacts) (Table 2); sallier-canopy foraging species, however, comprised the next most common foraging guild (36.4% of total contacts). About one-third (35.2%) of the breeding bird community consisted of common species. The five most abundant species based on the total number of contacts were Common Yellowthroat (*Geothypis trichas*), Red-eyed Vireo (*Vireo olivaceus*), Indigo Bunting (*Passerina cyanea*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), and Song Sparrow (*Melospiza melodia*). The vireo and the bunting were sallier-canopy foragers, whereas the other three were ground-shrub foragers.

As in winter, type-1 habitat was used more than expected by ground-shrub foraging species in the breeding seasons (Table 2); based on all breeding seasons combined, this habitat was avoided by sallier-canopy foragers. Species occurring more than expected in type-1 habitat were Gray Catbird (*Dumetella carolinensis*), American Redstart (*Setophaga ruticilla*), Common Yellowthroat, Common Grackle (*Quiscalus quiscula*), American Goldfinch (*Carduelis tristis*), and Song Sparrow; species less likely to occur in this habitat were Red-eyed Vireo, Ovenbird (*Seiurus aurocapillus*), Scarlet Tanager (*Piranga olivacea*), and Rufous-sided Towhee. Type-2 and type-3 habitats generally were used in proportion to their availability by the breeding bird community; however, some species, e.g., Common Yellowthroats, used these habitats more than expected, and others, e.g., Ovenbird, used these habitats less than expected. Type-4 habitat was avoided by ground-shrub foraging species, including Gray Catbird, American Redstart, Common Yellowthroat, Common Grackle, Northern Cardinal, Indigo Bunting, Rufous-sided Towhee, and Song Sparrow; only the Ovenbird used type-4 habitat more than expected.

Discussion.—The wintering bird community in my study essentially consisted of two major guilds, ground-shrub and trunk-bark foragers, each exhibiting preferential use of the different habitat types. Ground-shrub foragers, particularly Dark-eyed Juncos and White-throated Sparrows, were prevalent along forest edges (type-1 habitat), perhaps because of the availability of abundant weed seeds as a food resource (Rollfinke and Yahner 1990). In contrast, these species were absent from nearby forest stands managed by an even-aged system of clear-cutting, which were located about 10 km from the study site (i.e., Barrens Grouse Habitat Management Study Area [HMA]), because of a paucity of weed seeds in winter (Yahner 1986, 1993).

Although trunk-bark foragers, e.g., Black-capped Chickadee, Tufted Titmouse, and Downy Woodpecker formed wide-ranging interspecific flocks (Rollfinke and Yahner 1991a), this guild preferred type-2 habitat for at least two reasons. First, pitch pine in this habitat type was an important foraging substrate for trunk-bark foragers (Yahner 1987, Rollfinke and Yahner 1991b); pitch pine and other rough-barked trees have numerous crevices used as hiding places by arthropods which serve as food for wintering birds (e.g., Jackson 1979, Brawn et al. 1982). Second, compared with deciduous trees, conifers likely provided a more favorable microclimate for birds by reducing windchill and energetic costs while foraging during winter. As in nearby managed forest stands at the Barrens Grouse HMA (Yahner 1986, 1993), ground-shrub and saller-canopy foragers in the present study were the predominant guilds during the breeding seasons. Because most ground-shrub foraging species were found in type-1 habitat and less so in type-2 and type-3 habitats of the irrigated sector, distance to a forest edge probably was a major factor influencing the distribution of this guild. Strelke and Dickson (1980) and Yahner (1987), for example, noted that many forest birds adapted to edge and brushy conditions created by forest clear-cutting typically occurred within 25 m of the forest edge; sampling points in type-1 habitat usually were located about this distance from an edge.

Another factor affecting abundance and distribution of ground-foraging species was the presence of a lush, herbaceous layer of vegetation throughout the irrigated sector on the study area. Although several ground-foraging species in my study are considered edge species, such as Gray Catbird and Common Yellowthroat, and typically occupy habitat with dense understory vegetation (e.g., Forman et al. 1976; Whitcomb et al. 1981; Yahner 1991, 1993), they were relatively abundant throughout the irrigated sector (types 1–3) not only in type-1 habitat but also in types 2 and 3. Conversely, these species were scarce or absent in type-4 habitat which lacked a dense layer of herbaceous vegetation near ground level. On the other hand, one ground-shrub foraging species, the Ovenbird, was characteristic of type-4 habitat, probably because of reduced herbaceous growth. The Ovenbird is principally a forest-interior species (see Whitcomb et al. 1981, Yahner 1993), but while foraging it utilizes forest floors that lack abundant herbaceous cover (e.g., see Kahl et al. 1985, Holmes and Robinson 1988, Mulvihill 1992). Therefore, my findings suggest that the Ovenbird was the only species whose distribution and relative abundance were affected detrimentally by wastewater irrigation (see also Lewis and Sampson 1981, Rollfinke and Yahner 1990). In addition, a previous study found that Wood Thrushes (*Hylocichla mustelina*) were affected negatively by irrigation because dense herbaceous vegetation near ground level likely reduced foraging efficiency (Rollfinke et al. 1990). Saller-canopy foraging species, such as Red-eyed Vireo and Scarlet Tanager, tended to favor habitat types away from forest edges (types 2–4) in my study because these species typically are area-dependent, forest-interior species (Whitcomb et al. 1981, Robbins et al. 1989).

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RICHARD H. YAHNER, *School of Forest Resources, The Pennsylvania State University, University Park, Pennsylvania 16802. Received 1 Sept. 1994, accepted 10 Jan. 1995.*

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Sequence of plumage evolution in the Standardwing Bird of Paradise.—The faded appearance of the plumage of the Standardwing Bird of Paradise (*Semioptera wallacii*), endemic to Halmahera and Bacan (Batjan) Islands (White and Bruce 1985), is unique within the Paradisaeidae. The dull, unbarred plumage of both sexes is primarily medium brown, darker on the mantle, fading to a pale buffy-white on the remiges (see Gilliard 1969, Cooper and Forshaw 1977). Males possess an iridescent green breast shield and a pair of remarkable elongated wing coverts on each wing. These plumage elaborations have long attracted the attention of ornithologists, while the remainder of the plumage, arguably more interesting in an evolutionary sense, has largely been ignored until Frith (1992).

The phylogenetic relationships of *Semioptera*, a monotypic genus, are poorly known and in dispute. Nearly two-thirds of the fifteen currently recognized genera in the Paradisaeidae (Beehler and Finch 1985, White and Bruce 1985) have been suggested as possible sister taxa of *Semioptera* by taxonomists (see Frith 1992). Given the incredible variety of plumages within this assemblage of genera, especially among males, it is not possible at this time to determine the plumage color and pattern of its ancestor. Nevertheless, several lines of evi-