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The influence of Yellow-bellied Sapsuckers on local insect community structure.— Natural communities consist of irregular patchworks of organisms whose relative abundances both reflect and influence environmental heterogeneity (e.g., Diamond and Case 1986, Cornell and Lawton 1992). Within a given habitat, any species that augments environmental patchiness is likely to influence the abundances of sympatric species. For instance, through their unusual foraging strategy, Yellow-bellied Sapsuckers (*Sphyrapicus varius*) create rich resource patches in the form of sapwells, and may thereby affect population densities and spatial distributions of many co-occurring species.

The Yellow-bellied Sapsucker feeds primarily on phloem and sap obtained through the excavation of sapwells. A sapwell consists of horizontal rows of shallow holes drilled into bark, into which sap flows (Tate 1973). Sapsuckers drill newer rows directly above older wells, producing a two dimensional array of shallow holes. While the volume and quality of sap flow depend on both the tree species and the daily rates of transpiration and photosynthesis (Foster and Tate 1966), flow can often be considerable and sap often contains 20–30% sucrose (Tate 1973). Insects comprising seven orders and 20 families have been found associated with sapwells (Foster and Tate 1966). Preferential orientation of insects toward rich resource patches may be manifest as increased abundance and/or diversity of nectivorous insect communities in close proximity to sapwells. Therefore, by serving as a focal point for insect aggregation, sapwells may influence the local community structure (i.e., absolute and relative abundances) of the nectivorous insect guild. The purpose of this study was to determine (1) whether sapsucker foraging influences local insect diversity and species richness and, if so, (2) which insect taxa are most strongly influenced by the presence of sapwells.

Study area and methods.—To determine whether the presence of sapwells influences the local insect community, insect visitation was monitored at 16 artificial sapwells located at the University of Michigan Biological Station (UMBS) in Cheboygan County, Michigan. Artificial sapwells were established in paper birch trees (*Betula papyrifera*) by using a 4.8 mm-($^3/_{16}$ inch) diameter steel punch to create an array of holes resembling an active sapwell. In addition, adjacent bark was roughened with sandpaper to simulate recent sapsucker attendance. A 1-liter plastic bottle containing 30% sucrose solution (intended to mimic natural birch sap; Tate 1973) was mounted 25 cm above each artificial sapwell. Surgical tubing was run from the mouth of the bottle to the sapwell and drip rate was manipulated to simulate natural sap flow.

Eight sets of sapwells were established, each located in a separate sapsucker territory. Each set consisted of one active natural sapwell, and a pair of artificial sapwells (sampling stations), one located on a birch tree approximately 5 m from the natural sapwell and a second located on a birch tree approximately 40 m from the same natural sapwell. The near artificial sapwell sampled the insect community in close proximity to a natural sapwell, while the far artificial sapwell sampled the insect community far from a natural sapwell. Paired artificial sapwells were located in similar microhabitats and microclimates resembling those of the natural sapwells.

Each artificial sapwell was observed for one 20-min interval on each of 11 days between 25 July and 7 August 1992. Pairs of artificial sapwells were visited in random sequence. During each sample period, the number and identity of all insects visiting each artificial sapwell was recorded. Care was taken to avoid counting any individual more than once. When necessary, representative specimens were collected for subsequent identification. The majority of specimens was identified to family, and in all cases specimens were identified to the lowest possible taxonomic category permitted by the authors' expertise.

To determine whether artificial sapwells accurately mimicked natural sapsucker sapwells, insect visitation was also observed at two additional active natural sapwells in separate territories. Observational methods at natural sapwells were identical to those at artificial sapwells except that natural sapwells were visited on only three days.

To determine whether sapsuckers influence local insect community structure, total insect visits were compared between the near and far artificial sapwells of each pair, using paired *t*-tests. For the entire assemblage of insects visiting each artificial sapwell, we calculated four measures (1) a Shannon-Weiner diversity index (H′), appropriate because a small subset of the entire insect community was sampled; (2) evenness or relative diversity (J′), calculated as the ratio of the observed diversity to the maximum possible, given the same number of species; (3) species richness, defined as the total number of species observed; and (4) total number of individuals observed. In addition, we used Chi-square analysis to determine whether the relative abundances of insect species differed between areas near to vs far from a natural sapsucker sapwell. Where necessary, species containing few individuals were lumped into higher taxa, e.g., family or order.

Results.—A total of 2227 insects was observed during this study (1351 at artificial sapwells near to a natural sapwell and 876 at artificial sapwells far from a natural sapwell). The total number of visiting insects was significantly higher at artificial sapwells located near to a natural sapwell ($P = 0.035$; Table 1). Similarly, species richness was significantly higher and evenness was nearly significantly higher at near than at far artificial sapwells ($P = 0.002$ and $P = 0.083$, respectively; Table 1). In contrast, species diversity did not differ significantly between near and far artificial sapwells ($P = 0.18$; Table 1).

Differences in community composition were also evident from inspection of individual

TABLE 1

CHARACTERISTICS OF INSECT COMMUNITIES NEAR TO AND FAR FROM NATURAL SAPWELLS[a]

Characteristic	Near sapwells	Far sapwells	Paired *t*-statistic	*P*-value
Total number of individuals	168.9	109.5	2.61	0.035
	(60.8)	(27.2)		
Species richness	11.8	6.4	4.68	0.002
	(1.9)	(4.4)		
Diversity (H′)	0.45	0.39	1.49	0.180
	(0.15)	(0.13)		
Evenness (J′)	0.43	0.29	2.02	0.083
	(0.09)	(0.10)		

[a] Means are given with standard deviations in parentheses. Sample size was eight for each sapwell location.

species and species groups. Relative abundances of insect species differed significantly between near and far artificial sapwells ($P < 0.0005$; Table 2). Coleoptera, Diptera (exclusive of the Tephritidae), bald-faced hornets, and particularly Lepidoptera were more abundant than expected near to a natural sapsucker sapwell. In contrast, Collembola, Psocoptera, and ants were less abundant than expected near to a natural sapsucker sapwell (Table 2). In

TABLE 2

TOTAL NUMBER OF INDIVIDUALS FOR COMMON INSECT TAXA AT NEAR AND FAR SAPWELLS[a]

	Total number of individuals		
Taxon	Near sapwells	Far sapwells	Partial χ^2
Lepidoptera			
Tortricidae	16	0	10.39
Mourning Cloaks (*Nymphalis antiopa*)	10	0	6.39
Misc. Lepidoptera	14	3	3.37
Hymenoptera			
Yellow jackets (*Vespula* spp.)	854	574	0.44
Bald-faced hornets (*Dolichovespula* spp.)	63	27	3.28
Formicidae	313	229	1.94
Misc. Hymenoptera	11	7	0.00
Diptera			
Tephritidae	11	6	0.12
Misc. Diptera	26	6	5.70
Coleoptera	17	3	5.02
Psocoptera	11	12	1.64
Collembola	5	9	3.67
Total	1351	876	41.96

[a] Relative abundances differed significantly among sapwell locations ($\chi^2 = 41.96$, df = 11, $P < 0.0005$).

addition, one order and 20 families were observed near to but not far from natural sapwells; of these, seven families were observed also at natural sapwells. Six families were observed far from but not near to natural sapwells; however, of these, only one family was observed at natural sapwells (Table 3).

Discussion.—The results of this study suggest that the presence of Yellow-Bellied Sapsuckers can strongly influence local insect community structure. We observed significantly higher numbers of individuals and species richness, and nearly significantly higher species evenness, at artificial sapwells near to natural sapsucker sapwells compared to similar artificial sapwells that were far from natural sapsucker sapwells. Moreover, these differences were observed despite a generally conservative experimental design; for instance, the significantly higher total number of insects at near vs far artificial sapwells arose in spite of potential competition between natural sapwells and near (but not far) artificial sapwells.

Sapsucker sapwells represent a rich resource patch that is exploited by a wide variety of insect species, families and orders. We observed 14 families associated with natural sapwells; to our knowledge only 11 families have previously been reported (Bolles 1891; Nickell 1956, 1965; Foster and Tate 1966). Most observed taxa are nectivorous, with the exception of Collembola, which are generally associated with fungi and decaying wood. Of particular interest, sap beetles (Coleoptera: Nitidulidae) were observed only at natural sapsucker sapwells and at nearby artificial sapwells. Sap beetles feed exclusively on decaying fruit and fermenting plant juices, which appear to be scarce resources in most temperate forest habitats. This family may therefore depend on sapsuckers to augment an environment otherwise impoverished in such resources.

Foraging behavior varies considerably among the taxa of insects observed exploiting our artificial sapwells. The considerably higher relative abundance of Hymenoptera (particularly vespid wasps and ants) at near vs far sapwells (63% vs 23%) may indicate the importance of learning in this group. Artificial sapwells in close proximity to natural sapsucker sapwells may have been more rapidly discovered and therefore more often visited during this study. Presumably, learning-based site fidelity by these Hymenoptera was more influential than their ability to disperse over reasonable distances. Similarly, Lepidoptera are capable of learning information that allows increased foraging efficiency (Lewis 1988) and, despite their well-developed dispersal capacity, also displayed greater relative abundances at near vs far sapwells (2.96% vs 0.003%; Table 2).

Many patch-foraging insect species exploit a single patch until the resource is nearly exhausted (Heinrich 1979). A sapsucker sapwell is a rich and generally scarce resource patch. The spatial distribution of sapwells in northern forest habitats may therefore favor short-term, intensive patch exploitation (Real 1991).

Our results suggest that natural Yellow-bellied Sapsucker sapwells are a rich resource patch actively exploited by a wide variety of insect species. Similarly, Ehrlich and Daily (1988) and Daily et al. (1993) have shown that sapwells of the Red-naped Sapsucker, *Sphyrapicus nuchalis,* provide nourishment to over 40 insect species within subalpine Rocky Mountain ecosystems. Together, these observations indicate that, across a variety of habitats, the presence of sapsuckers may strongly influence the size, composition, and spatial distribution of local insect communities, just as they can influence the structure of local bird communities (Miller and Nero 1983, Daily et al. 1993).

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TABLE 3

INSECT TAXA IDENTIFIED DURING AT LEAST ONE SAMPLING PERIOD FROM NATURAL, NEAR AND FAR SAPWELLS

	Sapwell location		
Family/species	Near	Far	Natural
Lepidoptera			
Argyresthiidae	×		
Geometridae	×		
Itame pastularia		×	
Noctuidae	×	×	
Catacala ilia			×
Nymphalidae	×		
Limenitis arthemis astyanax			×
Nymphalis antiopa			×
Nymphalis vau-album			×
Lethe anthedon		×	
Tortricidae	×		
Satyridae			×
Microlepidoptera	×	×	
Hymenoptera			
Apidae		×	
Braconidae	×		
Chrysididae	×		×
Formicidae	×	×	×
Ichneumonidae		×	
Pompilidae	×	×	
Sphecidae	×	×	
Tiphiidae	×		
Tiphiinae sp.		×	
Vespidae			
Vespula sp.	×	×	×
Diptera			
Calliphoridae	×		×
Dolichopodidae	×		×
Drosophilidae			×
Lauxaniidae		×	
Heleomyzidae	×		
Milichiidae			×
Muscidae (2 spp.)	×		×
Psocidae		×	
Sciuridae	×		
Tachinidae	×		
Tephritidae	×	×	×

TABLE 3
CONTINUED

Family/species	Sapwell location Near	Sapwell location Far	Natural
Coleoptera			
Cantharidae	×		
Carabidae			
Calosoma sp.	×		
Curculionidae	×		×
Dermestidae			
Trogoderma sp.			×
Elateridae		×	
Nitidulidae (3 spp.)	×		×
Scarabacidae			
Osmoderma sp.	×		
Scolytidae		×	
Silphidae			
Silpha sp.	×		
Hemiptera			
Pentatomidae		×	
Homoptera			
Membracidae	×		
Collembola			
Eutomobryidae	×	×	
Psocoptera			
Psocidae	×	×	

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Diurnal activity budgets of pre-nesting Sandhill Cranes in arctic Canada.—Lack (1968) contended that waterfowl clutch size evolved in relation to female food consumption during egg formation. Ryder (1970) modified this hypothesis noting that several arctic-breeding geese did not feed during egg-laying. Those geese probably used nutrients accumulated on wintering and staging areas to lay and incubate clutches (Ankney and MacInnes 1978, Raveling 1979). More recent studies of endogenous reserves and the amount of time spent feeding when at, or near to, the ultimate breeding areas before clutch initiation have suggested that this simple model does not apply to all populations (e.g., Greater White-fronted Geese [*Anser albifrons*], Fox and Madsen 1981, Budeau et al. 1991; Canada Geese [*Branta canadensis*], Bromley and Jarvis 1993), even geese breeding in the high arctic (e.g., Snow Geese [*Anser caerulescens*], Gauthier and Tardif 1991).

Sandhill Cranes (*Grus canadensis*) allocate less nutrients to clutch formation in relation to body size than northern nesting geese (ca 7% vs 17%, Bromley, unpubl. data), and generally are believed to acquire necessary nutrients for migration and reproduction at spring staging areas (Krapu et al. 1985). This enables arriving cranes to cope with highly variable weather conditions encountered on arctic breeding areas and initiate clutches with minimal local exogenous supplement to their nutrient reserves.

Both Sandhill Crane sexes share incubation. As female cranes contribute comparatively less nutrient investment to the clutch and to incubation than geese, we hypothesise that there is less male investment in vigilance and female protection, more time spent in maintenance or improvement of condition by the male and less time feeding by females than in arctic nesting geese. During a study of pre-nesting waterfowl in the central Canadian Arctic, we tested the predictions that: (1) male cranes feed less and spend more time alert than females, but that the differences would be less marked than among arctic nesting geese, and (2) the nesting phenology of cranes precede that of locally breeding Greater White-fronted and Canada geese because: (1) most of the cranes' reproductive material is endogenously de-