COMPETITION AMONG BARK-FORAGING BIRDS IN CENTRAL ILLINOIS: EXPERIMENTAL EVIDENCE

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Most studies on similar coexisting species enumerate ecological differences which presumably reduce the demand for common resources and allow coexistence (MacArthur 1958, Root 1967, Stallcup 1968). As Schoener (1974) pointed out, however, these differences alone do not demonstrate the role of competition in structuring avian communities. Even if niches were arranged randomly with respect to one another, differences would exist. Observational studies can reveal very little about how avian species influence one another except when direct aggressive interactions are observed. Experimental evidence is needed to more fully understand community organization as suggested by Reynoldson and Bellamy (1974), Colwell and Fuentes (1975) and Connell (1975). Thus, observation is useful as a first step to suggest hypotheses, which then need to be tested.

Reynoldson and Bellamy (1974) suggested that manipulation of species in a community is the best way to discover if competitive interactions affect use of niche space. By removing birds during the breeding season, others have shown that conspecifics may limit breeding space (Stewart and Aldrich 1951, Orians 1961, Jenkins et al. 1964, Holmes 1966). Davis (1973) trapped birds for three winters and determined that Golden-crowned Sparrows (*Zonotrichia atricapilla*) used a willow thicket area more than Dark-eyed Juncos (*Junco hyemalis*). During the winter of the fourth year, he removed the sparrows and found a significant shift in habitat use by the juncos.

The guild of bark-foraging birds in deciduous forests of central Illinois during winter includes the Red-headed Woodpecker (*Melanerpes erythrocephalus*), Red-bellied Woodpecker (*Melanerpes carolinus*), Downy Woodpecker (*Picoides pubescens*), White-breasted Nuthatch (*Sitta carolinensis*), and Brown Creeper (*Certhia familiaris*). In another study (Williams and Batzli 1979b), we followed a natural experiment in which the dominant member of the guild (Red-headed Woodpecker) was absent during one winter but present in the next. When these woodpeckers occupied our upland study areas during winter, Red-bellied Woodpeckers used lowland areas where Red-headed Woodpeckers were much less abundant. When Red-headed Woodpeckers vacated our upland study areas during one winter because of a mast failure, Red-bellied Woodpeckers freely foraged over our entire upland study site. Similarly, in winters with Red-headed Woodpeckers present, we found Downy Woodpeckers foraging low in the canopy, but in winters when Red-headed Woodpeckers were absent, Downy Woodpeckers tended to forage higher. Here we report the results of a controlled experiment designed to test the following hypotheses generated from these earlier studies: (1) The aggressive actions of Red-headed Woodpeckers prevent Red-bellied Woodpeckers from using upland habitat during the winter. (2) Red-headed Woodpeckers constrain Downy Woodpeckers to forage lower in the canopy in upland areas. (3) Red-headed Woodpeckers also prevent White-breasted Nuthatches from using some upland habitat.

THE BIRDS

The Red-headed Woodpecker is the only interspecifically territorial species of the guild during winter. In the fall, these birds bring acorns, corn, and often seeds to their territories (0.2–0.8 ha), pound them into pieces at "anvil" sites, and place them in natural crevices in and under bark. These caches are aggressively defended against competitors throughout the season.

The Red-bellied Woodpecker resembles the congeneric Red-headed Woodpecker morphologically and behaviorally (Bent 1939, Peters 1948, Mayr and Short 1970) and likewise depends upon mast and seeds for its main winter food. On the other hand, the Red-bellied Woodpecker does not store mast as extensively; it does not defend stored mast from other species but distributes food items over a broad individual feeding area (2–6 ha; Kilham 1963), and it feeds to a limited extent on woodboring larvae in the winter (Beal 1911).

The Downy Woodpecker generally feeds

on insects during winter, although some vegetable foods such as mast, corn, and other seeds are eaten (Beal 1911, Williams and Batzli 1979a). It does not cache food items, but forages over an area as large as that of the Red-bellied Woodpecker.

The White-breasted Nuthatch primarily exploits vegetable foods throughout the non-breeding season (Williams and Batzli 1979a). Winter feeding areas are not defended even though some food items are stored. Lacking the long protrusible tongue of woodpeckers, it forages by probing behind bark and into shallow crevices.

The Brown Creeper overwinters in the contiguous 48 states and migrates northward to breed. It usually forages on large tree trunks and limbs for small insects. Because this species rarely occurred on our study areas during this experiment, it is not considered further in our analysis.

STUDY AREAS AND METHODS

A patch of timber, 800 m × 300 m, situated along the Sangamon River near Mahomet, Illinois, was selected for this investigation. Because this wood contains two rather similar upland areas separated by a lowland floodplain (Fig. 1), it presented an opportunity for experimentation. For both study areas, frequency, density, and basal area of trees were determined by the point-center-quarter technique as suggested by Cottam et al. (1953).

The southern upland area (5.9 ha), "Monen upland," was dominated by white, black, and red oak (Table 1). Black and red oaks were the largest trees in the stand, with an average basal area per tree of 0.52 m². Elms, ash, black cherry, sassafras, hackberry, and redbud trees composed the understory. Our second study site, "Hart upland" (9.6 ha), lay in the northern part of the woods and was also dominated by white, black, and red oaks. Williams (1977) included a more detailed analysis of this area.

Vertical structure was measured, using a modification of the technique described by Emlen (1967), during December when foliage was absent. At each point on a 25 × 25 m grid, a circular tube (30 cm long, 4 cm in diameter) was used to view limbs and branches along a path perpendicular to the ground. Presence or absence of each limb size category was scored for each height interval as viewed through the tube. Height intervals were determined by a forester's altimeter. The vertical structures of the study areas were similar (Fig. 2).

Because some birds, especially Downy Woodpeckers, sometimes foraged on fallen logs, lengths and diameters for logs greater than 5 cm in diameter were measured in 10 randomly chosen 25-m² quadrats in order to assess their availability. Results were similar for Hart and Monen (Table 2).

In order to test our hypotheses regarding the role of Red-headed Woodpeckers in community organization, we removed these birds from Monen upland during the winter of 1974–75 and compared niche parameters of the other guild members before and after the experiment. Red-headed Woodpeckers were not removed from Hart upland, which served as a
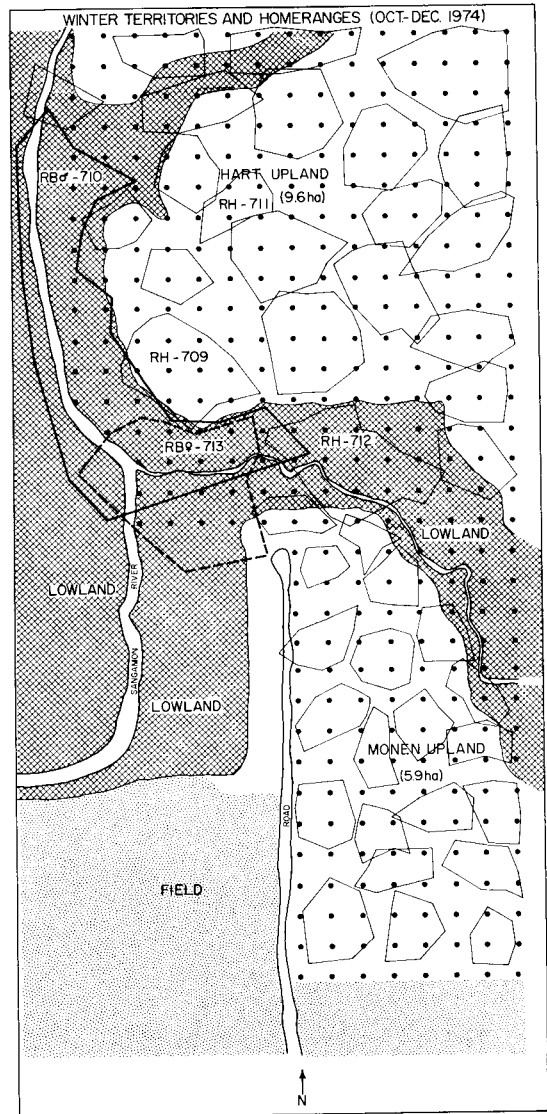

FIGURE 1. Territories for Red-headed Woodpeckers and feeding areas for Red-bellied Woodpeckers in Hart and Monen uplands before manipulation. Grid markers are 25 m apart. Our lowland area comprised 3.4 ha. Our grid occupied the entire upland area for both woods, but not the lowland.

control area. In the fall of 1975 the mast crop was poor and Red-headed Woodpeckers emigrated. This allowed comparison of results when Red-headed Woodpeckers were artificially and naturally removed.

Each area was divided into 25-m² quadrats (Fig. 1). Territories and home ranges were mapped for birds in both areas beginning 1 December 1977, by following each bird encountered and recording on a base map all movements and aggressive encounters. Several individuals of each species were banded and color-marked to facilitate measurement of movements. All Red-headed Woodpeckers in Monen Woods were shot between 24 December 1974 and 1 January 1975. We censused each area before and after manipulation.

We determined usage in terms of five niche dimensions: (1) activity of bird; (2) tree species occupied;

TABLE 1.   Vegetation analysis of Monen upland (M) and Hart upland (H).[a]

Vegetation type	Relative density		Relative dominance		Basal area/tree	
	M	H	M	H	M	H
Black oak, red oak (*Quercus velutina, Q. rubra*)	11.6	19.5	33.6	58.1	.52	.38
White oak (*Q. alba*)	36.4	27.7	55.3	34.6	.14	.10
Elm spp. (*Ulmus rubra, U. americana*)	18.2	27.2	2.2	2.2	.01	.01
Standing dead trees	11.6	0.5	7.5	0.1	.06	.01
Ash (*Fraxinus americana*)	1.9	1.0	0.1	0.1	.01	.01
Mockernut hickory (*Carya tomentosa*)	1.9	1.9	0.1	0.4	.01	.02
Shagbark hickory (*C. ovata*)	0.5	1.4	+	0.2	+	.01
Bitternut hickory (*C. cordiformis*)	0.5	0.5	+	2.0	+	.33
Hop-hornbeam (*Ostrya virginiana*)	0.9	—	+	—	+	—
Black cherry (*Prunus serotina*)	6.0	7.7	0.4	1.3	.01	.01
Sassafras (*Sassafras albidum*)	10.2	11.0	0.6	0.9	.01	.01
Basswood (*Tilia americana*)	—	0.5	—	0.1	—	.02
Hackberry (*Celtis occidentalis*)	—	0.5	—	+	—	+
Redbud (*Cercis canadensis*)	—	1.0	—	+	—	+
Total density (no./ha) and basal area (m²/ha)	553.7	565.3	16.43	19.83		

[a] Plus signs (+) indicate values < 0.1 for relative dominance and < 0.01 for basal area/tree.

(3) height of bird in tree; (4) substrate dead or alive; and (5) limb diameter. At a signal emitted every 10 s from an electronic metronome (after Wiens et al. 1970), a bird was scored for each dimension. No bird was observed for more than 5 min at a time to reduce bias.

We placed activities in one of the following categories (modified from Ficken and Ficken 1966, Jackson 1970, and Willson 1970): (1) Perch—no evident behavior occurring; (2) Scale—pedal locomotion (horizontal or vertical) usually in search of food; (3) Drill—stationary percussion; (4) Bark Probe—poking bill into cracks and crevices of bark; (5) Unknown—behavior unobservable at the signal; (6) Fly—bird in flight; (7) Pound—repeated hammering of food item, usually acorns or corn; (8) Ground Forage—motion along ground in search of food; (9) Acorn Harvest—sequestering acorns either from trees or the ground; (10) Acorn Storage—placing acorn pieces into crevices within the territory; (11) Other—any other activity such as display, preen, etc.

Foraging activity graphs were constructed using relative amounts of time spent on different foraging tactics. Perching is included in these graphs because birds stop while foraging and examine the bark surface. Hawking was included because Red-headed Woodpeckers occasionally (i.e., less than 1% of their time) hawk aerial insects from perched positions on warm winter days.

We estimated height visually for each bird, often using a forester's altimeter for birds at higher levels. For estimating limb diameters we used the size of the bird being observed as a reference.

Niche breadths (B_i), or tendencies to specialize along a particular resource dimension, were calculated using Levin's (1968) formula:
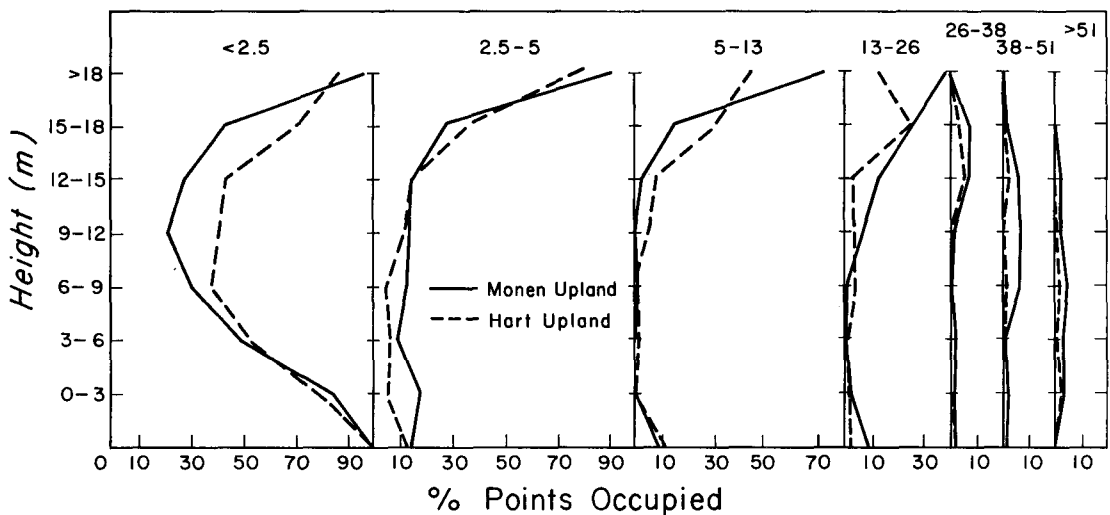
$$B_i = 1/\Sigma P_i{}^2(n)$$

FIGURE 2.   Comparison of the vertical structure (percentage of points occupied for each height category) for Hart and Monen upland areas. Numbers at top represent different categories of limb sizes (diameter in centimeters).

TABLE 2. Percent of observations on different tree species for the bark-foraging guild after manipulation and availability of trees. Numbers of observations in parentheses.[a]

Type of tree	Red-headed Woodpeckers Hart 1975 (819)	Red-bellied Woodpeckers Monen		Downy Woodpeckers Hart 1975 (918)	Monen		White-breasted Nuthatch Monen		Availability (relative basal area)	
		1975 (178)	1976 (380)		1975 (1129)	1976 (479)	1975 (169)	1976 (121)	Hart	Monen
Black oak, red oak	45	47	46	28	9	11	9	10	53	47
White oak	47	51	54	50	91	86	91	89	31	39
Understory trees	4	—	—	11	—	2	—	—	10	2
Fallen logs	+	—	—	3	—	1	—	—	5	7
Shagbark hickory	1	—	—	7	—	—	—	—	+	+
Standing dead	—	1	—	+	—	—	—	1	+	5
Other	3	1	—	1	—	—	—	—	1	+

[a] Plus signs (+) indicate values < 0.5.

where P_i is the proportion of observations in the ith unit of the resource set and n equals the number of resource states. To simplify comparison of niche breadth values where different numbers of categories were involved, we scaled the values (Fager 1972) so that $B_{max} = 1$ and $B_{min} = 0$.

Overlap values on each niche dimension were calculated using Schoener's index (1968):

$$O_{xy} = 1 - \tfrac{1}{2} \Sigma \, |P_{xi} - P_{yi}|$$

where P_{xi} and P_{yi} are proportions of time spent for the xth and y^{th} species in the ith resource state. Total overlap along a dimension yields a value of one; complete separation yields a value of zero. As Colwell and Futuyma (1971) pointed out, it is difficult to interpret overlap values as direct measures of competition. We use them here to indicate niche dimensions along which competition may occur.

Interspecific comparisons were made on frequency of observations by chi-square contingency analysis. Sample means for territory size and morphological data were compared using a t-test. Only trends with a probability of less than 0.05 are discussed below.

RESULTS

BEFORE MANIPULATION

We recorded 18 and 20 Red-headed Woodpeckers on our control and experimental areas, respectively, during December before manipulation. In addition, four Downy Woodpeckers used Hart upland, whereas five Downy Woodpeckers used Monen. Red-bellied Woodpeckers were not seen in either upland area. A single White-breasted Nuthatch was seen in Monen upland before manipulation.

Territories and home ranges before manipulation are shown in Figure 1. Average territory size of Red-headed Woodpeckers in Hart upland was 0.38 ± .04 ha (± 1 SE), whereas for Monen it was significantly smaller (0.17 ± .04 ha; $P < 0.05$). Red-bellied Woodpeckers occurred only in the lowland. Birds of both species were trapped, banded and color-marked; and their home ranges were mapped (Fig. 1).

Red-headed Woodpeckers occupied the higher zones in both Hart ($\chi^2 = 117.0$, $P < 0.005$) and Monen woods ($\chi^2 = 89.0$, $P < 0.005$), whereas, Downy Woodpeckers concentrated in the lower zones (Fig. 3). Both species preferred oak trees and live substrate, but Downy Woodpeckers used smaller branches and drilled and probed more than Red-headed Woodpeckers. We found two significant differences between birds in Monen and Hart. White oaks and dead trees were used more often in Monen by both Red-headed Woodpeckers ($\chi^2 = 53.2$, $P < 0.005$) and Downy Woodpeckers ($\chi^2 = 30.3$, $P < 0.005$), apparently because more were available there. In all other respects, foraging behavior was similar in both woods.

AFTER MANIPULATION

After Red-headed Woodpeckers had been removed, the marked pair of Red-bellied Woodpeckers which had previously inhabited the lowland now occupied all of Monen upland (Fig. 4). Furthermore, we observed four White-breasted Nuthatches foraging in Monen but none in Hart. The densities of Downy Woodpeckers for both areas were unchanged. From census data taken in January 1976, we found the numbers of individuals of other species (Red-bellied Woodpeckers, Downy Woodpeckers, and White-breasted Nuthatches) in Monen during the winter of 1976 were similar to those of 1975 after manipulation.

Red-headed Woodpeckers and Red-bellied Woodpeckers foraged in similar ways (Fig. 5), suggesting high overlap in food habits. We calculated no differences between Downy Woodpeckers for the experimental and control areas or for years. Nuthatches searched over bark surfaces a large proportion
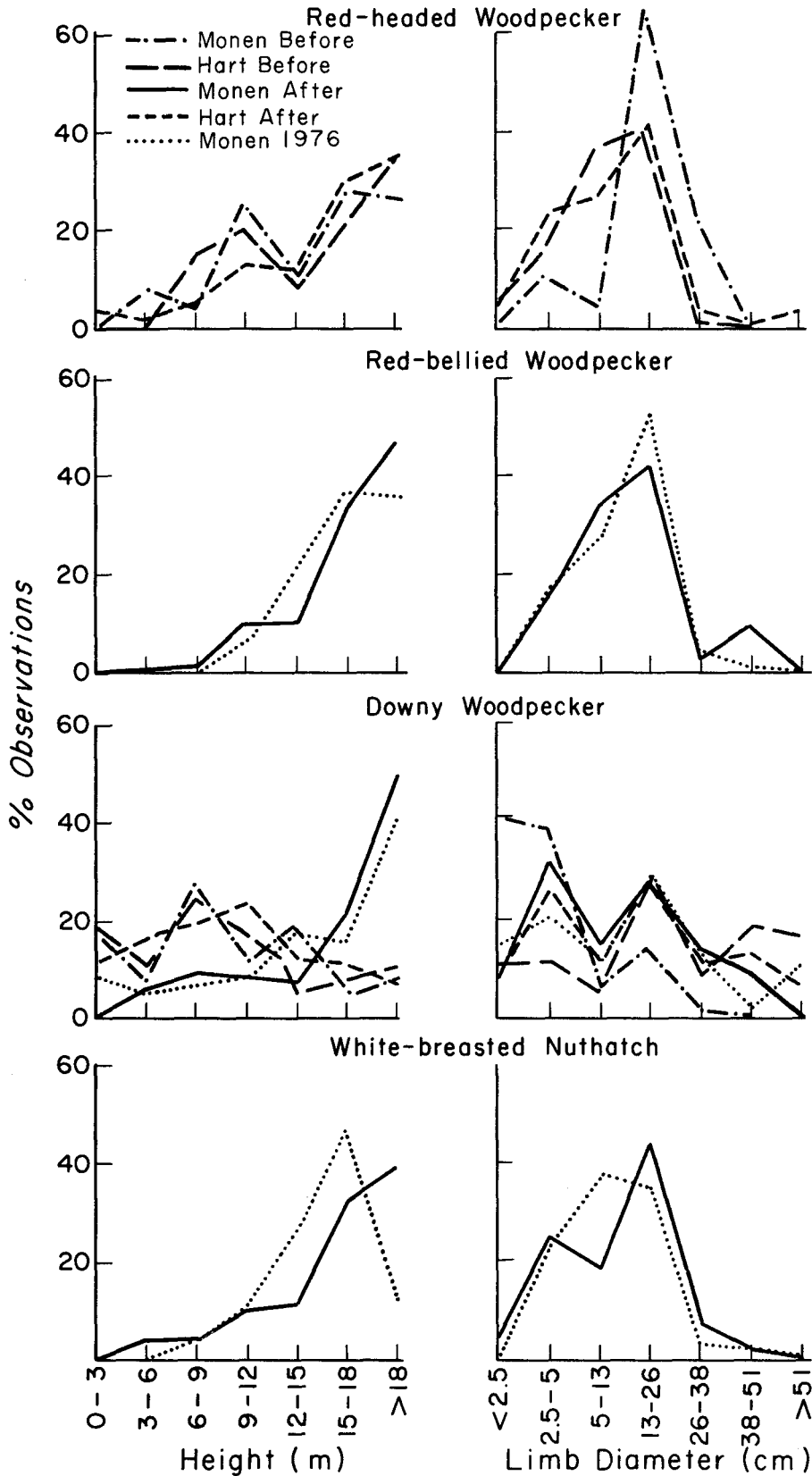
FIGURE 3. Percentage of observations for heights and limb diameters used by the bark-foraging guild before and after manipulation and in 1976 when Red-headed Woodpeckers naturally vacated the Monen upland.
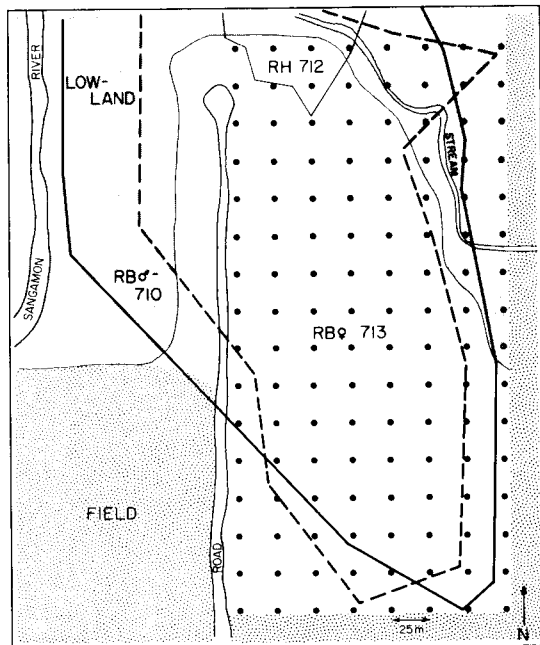
FIGURE 4. Feeding areas for Red-bellied Woodpeckers in Monen upland after removal of Red-headed Woodpeckers.
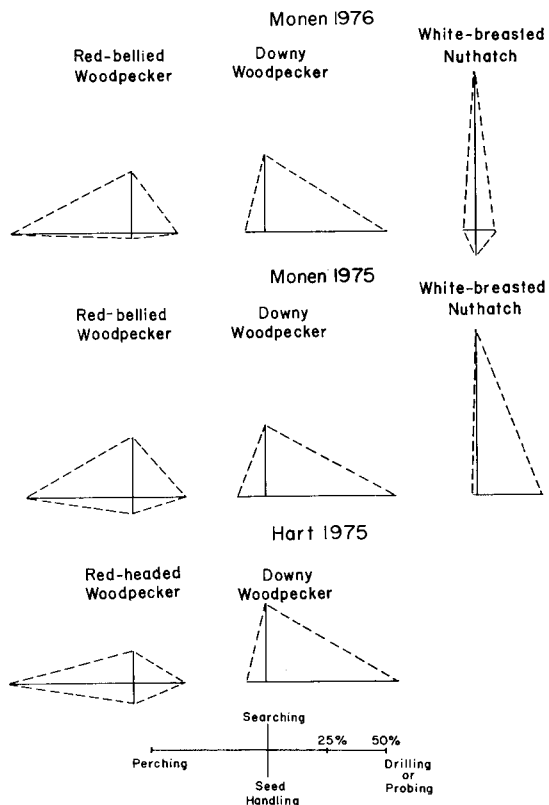

FIGURE 5. Percentage of time spent in different foraging activities for bark-foraging birds in experimental (Monen) and control (Hart) areas after removal, and in the Monen upland in 1976.

of their time for both winters in Monen, but spent more time handling seeds during 1976.

Species differed from the availability index and from each other in their use of trees on the two areas after manipulation (Table 2). Red-bellied Woodpeckers and Nuthatches in the experimental area and Red-headed Woodpeckers in the control area used oaks. Downy Woodpeckers searched white oak trees for food more in the experimental area. The following winter in Monen, Red-bellied Woodpeckers foraged in black and red oaks as well as white oaks; Downy Woodpeckers and White-breasted Nuthatches once again concentrated on white oak.

Upper portions of the canopy were occupied by Red-headed Woodpeckers in Hart, and by Red-bellied Woodpeckers and nuthatches in Monen (Fig. 3). Downy Woodpeckers in the experimental area used higher stations than in the control area where they made greater use of understory trees ($\chi^2 = 572.9$, $P < 0.005$). We obtained consistent results when Red-headed Woodpeckers naturally vacated Monen the following winter.

All species, except for Red-headed and Red-bellied woodpeckers during 1975 ($\chi^2 = 0.21$, $P > 0.05$), used live and dead substrates differently (Table 3). Nuthatches foraged on living trees more than did the other species. In 1976 Red-bellied Woodpeckers used dead substrate more than the previous year.

Red-headed Woodpeckers in Hart, and Red-bellied Woodpeckers and White-breasted Nuthatches in Monen, used limb categories in about the same proportions (Fig. 3). Downy Woodpeckers favored smaller limbs in both areas (Monen $\chi^2 = 187.7$, $P < 0.005$; Hart $\chi^2 = 207.3$, $P < 0.005$). Trends were similar for the following winter.

A comparison of niche breadths along the five dimensions for each species showed that White-breasted Nuthatches were the most specialized in Monen for both winters (Table 4). Downy Woodpeckers, overall generalists

TABLE 3. Dead substrate utilization for Hart upland in 1975 and for Monen upland in 1975 and 1976.[a]

Substrate	Hart upland		Monen 1975			Monen 1976		
	RH[b]	DW	RB[b]	DW	WBN	RB	DW	WBN
Alive	71	65	70	59	87	44	75	70
Dead	29	45	30	41	13	56	25	30

[a] Sample sizes the same as in Table 2. RH = Red-headed Woodpecker, DW = Downy Woodpecker, WBN = White-breasted Nuthatch.
[b] No significant difference ($P > 0.05$). All other species comparisons statistically significant ($P < 0.05$).

TABLE 4. Niche breadths along five dimensions for Hart upland (H) in 1975 and Monen upland in 1975 (M-75) and 1976 (M-76).

	Red-headed Woodpecker	Red-bellied Woodpecker	Downy Woodpecker	White-breasted Nuthatch
Activity				
H	.29	—	.35	—
M-75	—	.40	.35	.12
M-76	—	.52	.33	.26
Tree				
H	.14	—	.21	—
M-75	—	.11	.06	.04
M-76	—	.17	.15	.05
Height				
H	.55	—	.89	—
M-75	—	.32	.38	.44
M-76	—	.38	.45	.38
Dead or alive				
H	.70	—	.84	—
M-75	—	.72	.94	.30
M-76	—	.98	.60	.72
Limb diameter				
H	.41	—	.73	—
M-75	—	.38	.60	.40
M-76	—	.29	.74	.38
Mean				
H	.42	—	.60	—
M-75	—	.39	.47	.26
M-76	—	.47	.45	.36

for the winter of 1975 in both areas, had the highest mean breadth in the control area where Red-headed Woodpeckers were present. The following winter, Downy and Red-bellied woodpeckers had overall niche breadths of almost equal value in Monen.

The mean overlap value calculated for Red-headed Woodpeckers in Hart upland and Red-bellied Woodpeckers in Monen was 0.89. This value was higher than for comparisons between Downy Woodpeckers in the two areas (0.81), re-emphasizing the similarity between Red-headed and Red-bellied woodpeckers (Table 5).

TABLE 5. Niche overlap values along five dimensions for Red-bellied Woodpeckers (RB; from experimental area) and Red-headed Woodpeckers (RH; from control area), and for Downy Woodpeckers (DW) from both areas. Symbols as in Table 3.

Species	RB vs. RH	DW vs. DW
Forage activity	.86	.92
Tree species	.93	.79
Height	.84	.49
Dead or alive	.99	.94
Limb diameter	.85	.90
Mean	.89	.81

DISCUSSION

Our hypothesis that the aggressive actions of Red-headed Woodpeckers restrict exploitation of habitats by the Red-bellied Woodpecker is supported by our data. The habitat expansion by Red-bellied Woodpeckers in the experimental area after Red-headed Woodpeckers had been removed is strong evidence that their horizontal distribution was restricted by the socially dominant Red-headed Woodpecker. If Red-headed Woodpecker densities were low and this species did not occupy all of the upland, Red-bellied Woodpeckers could have occupied portions of the upland not taken by Red-headed Woodpeckers. However, during four years of investigation this did not happen. During the two years when Red-headed Woodpeckers were present in upland forest, Red-bellied Woodpeckers were not; but Red-bellied Woodpeckers were present both years when Red-headed Woodpeckers were absent.

Willson (1970) found some areas of central Illinois where Red-bellied Woodpeckers regularly intruded into the territories of Red-headed Woodpeckers, but the intruders were often displaced. Kilham (1963) also noted that during high mast years Red-headed

Woodpeckers inhabited Creek Wood, Maryland, but during low mast years Red-headed Woodpeckers would emigrate, and Red-bellied Woodpeckers would reside in the woods. These observations lend credence to our hypothesis that Red-headed Woodpeckers prevent Red-bellied Woodpeckers from using upland habitat. During winter, both species rely heavily on seeds and mast for food (Beal 1911, Williams and Batzli 1979b) and we have calculated a dietary overlap of 0.86. Red-headed Woodpeckers must exclude Red-bellied Woodpeckers from their territories in order to protect their winter food supply.

How, then, do Red-bellied Woodpeckers survive during winters of low mast production when Red-headed Woodpeckers cannot? We hypothesize that the fundamental niche, *sensu* Hutchinson (1957), of the Red-bellied Woodpecker is broader than that of the Red-headed Woodpecker. Apparently, Red-bellied Woodpeckers can overwinter in areas of low mast production by eating more insects as well as other vegetable material. Although culmen lengths of both species are similar (Williams 1977), their mean (±1 SE) tongue lengths are significantly different: 73.1 ± .7 mm (for RB) and 53.5 ± 1.1 mm (for RH). This probably would allow Red-bellied Woodpeckers to obtain insects not available to Red-headed Woodpeckers. In support of this idea, data from Beal (1911) showed wood-boring larvae in the diets of Red-bellied Woodpeckers during winter but very few such insects in stomachs of Red-headed Woodpeckers. Martin et al. (1951) found that diets of Red-bellied Woodpeckers consisted of 18% insects during winter, but Red-headed Woodpeckers had only 9%.

Our experimental results also support our hypothesis that Red-headed Woodpeckers force Downy Woodpeckers to forage lower in upland areas. Downy Woodpeckers take more arthropods during winter than do Red-headed Woodpeckers (Beal 1911, Williams and Batzli 1979a), but Downy Woodpeckers also consume vegetable resources such as mast and corn. Since Red-headed Woodpeckers primarily store mast and corn in the higher zones, Downy Woodpeckers are allowed to forage in the lower canopy away from the principal storage areas. After Red-headed Woodpeckers were removed from the experimental area, Downy Woodpeckers foraged higher. Such a shift may be a result of several factors. First, because Red-headed Woodpeckers had cached acorns in the higher zones, Downy Woodpeckers may have shifted upward to

exploit this undefended resource. Second, because more limbs and branches occur higher in the canopy, Downy Woodpeckers may have shifted upward to forage on a richer source of insects. Data from the 1976 winter, when Red-headed Woodpeckers were absent and few acorns were stored, suggest that the upward shift was not solely in response to availability of acorns.

Several authors have reported on the vertical distribution of Downy Woodpeckers in woodlands, but only a few have concurrently studied other species in the community. In nearby Brownfield Woods, Wilson (1970) found Downy Woodpeckers foraging below 10 m over 50% of the time during winter. Although she did not propose Red-headed Woodpecker dominance as the cause of such a pattern, this species was present on her study area.

Though less convincing, our results also support our hypothesis that the dominance of Red-headed Woodpeckers affects the distribution of White-breasted Nuthatches. Nuthatches were uncommon in Hart upland, but they moved into Monen Woods after we removed the Red-headed Woodpeckers.

When we observed nuthatches foraging in Hart upland, they usually were chased by Red-headed Woodpeckers. Home range data for nuthatches during the winter of 1974–75, when Red-headed Woodpeckers inhabited most of Hart upland, suggest that they foraged mostly in the lowland area where few Red-headed Woodpeckers had established territories (Williams 1977). Furthermore, since a large proportion of the winter diet of White-breasted Nuthatches is mast and corn (Bent 1948), the advantage to Red-headed Woodpeckers from excluding this species is clear. Nuthatches probably avoided the areas of Red-headed Woodpeckers because they could forage more efficiently in places where they were less likely to be chased. Furthermore, White-breasted Nuthatches store seeds, and it would be advantageous for them to maintain winter feeding areas in habitat unoccupied by a more dominant species.

Morse (1974) predicted that if an interspecific dominance hierarchy exists, subordinates should shift their use of resources so as to decrease their overlap with dominants. This change may consist simply of retreating from the area where the dominant is present, thus narrowing the niche of the subordinate; or, it may be accompanied by simultaneous expansion into areas not used when the dominant is absent, thereby broadening the
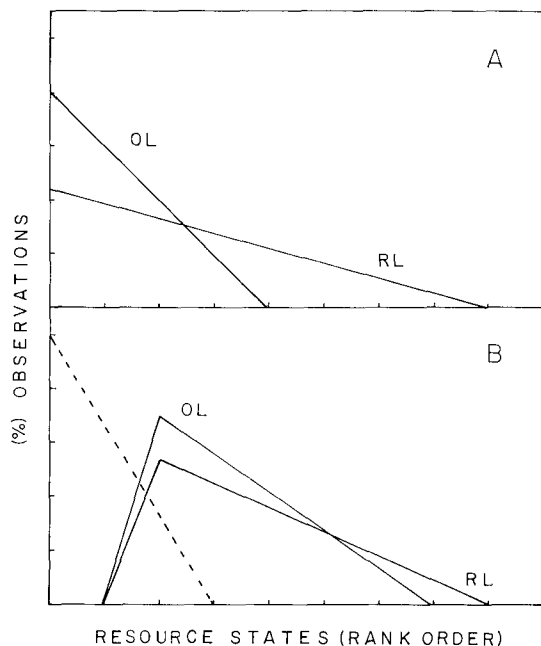
FIGURE 6. Graphic model of resource utilization by subordinate species (solid lines) in the absence (A) and presence (B) of a dominant (dashed line). Subordinate population may be limited by the resource graphed (RL) or by some other factor (OL).

subordinate's niche. Our results generally agree with this prediction but in a more complex way than originally envisioned. Two species, Red-bellied Woodpeckers and White-breasted Nuthatches, were limited in horizontal space (to the flood plain); Downy Woodpeckers were restricted along vertical space (to lower levels in the trees), but their niche breadth increased along the dimension (e.g., $B = 0.80$ before; $B = 0.38$ after in Monen). The dichotomy of responses probably is due to different patterns of resource exploitation. Downy Woodpeckers could forage lower in the canopy for insects, but Red-bellied Woodpeckers and nuthatches required more vegetable food than could be supplied by the lower zones.

Overlap between dominants and subordinates is usually associated with a decrease in niche breadth of the subordinate species (Colwell and Futuyma 1971, Morse 1974). Such a response indicates that the subordinate occupied a large portion of its fundamental niche before the dominant member appeared. In some studies, however, subordinate birds increased niche breadth along certain niche dimensions in the presence of dominants (Willis 1966, Morse 1970, Yeaton 1974).

Whether niche breadths of subordinate species should increase or decrease in the presence of dominants can be considered with the use of a graphic model (Fig. 6). Resource states along one dimension are ranked according to their value, a function of benefit/cost ratios. The proportion of observations of the species for each resource state are graphed so that the area under each curve equals one. Wider, lower curves represent greater niche breadth along the dimension shown. By definition, a species will take resources from more valuable states first, and, in the absence of competitors, curves of resource utilization will decrease monotonically.

In this situation, niche breadth of a species without competitors will depend upon population density. If the population is not limited by the resource in question (other-limited, OL), it will specialize on the more valuable resource states. When limited by the resource, it will utilize all profitable states and the niche will be broader (Fig. 6A).

Now suppose a dominant competitor monopolizes the most valuable resource states (Fig. 6B). Immediately after invasion, a subordinate species that is not limited by resources along the dimension OL will shift to less valuable resource states and also broaden its use of states to acquire the same quantity of resources (density remains unchanged). The niche of a resource-limited species (RL) must become narrower because it cannot expand to new resource states; this portion of its fundamental niche is already occupied. Hence, density-dependent mortality will increase, and the population will decline.

When the dominant is removed, both species types (OL and RL) will initially decrease their niche breadths; the species that is other-limited will assume its previous breadth, and since the density of the RL species has decreased, the niche of the other-limited form will be narrower than before. Only after reproduction or immigration will the resource-limited species reoccupy the entire niche dimension.

We therefore conclude that the response of a subordinate species to the presence or absence of a dominant competitor is not predictable without an intimate knowledge of the critical resource dimensions and how the species exploit them. The expansion of Red-bellied Woodpeckers and White-breasted Nuthatches into upland habitats may represent an increase in their niche breadth, suggesting that their populations were limited by space. Yet, these birds could have decreased their niche breadth along the food dimension by concentrating on the caches of Red-headed Woodpeckers. On the other hand,

the high niche breadth of Downy Woodpeckers along height, tree species, and limb diameter in the presence of Red-headed Woodpeckers suggests that Downy Woodpeckers were forced to forage in less productive areas over a larger array of foraging sites in order to obtain enough food and that their population was not limited along these dimensions.

Our model and data also show that even if two species overlap little along one dimension, they may still compete strongly. If they are not seen to damage one another directly, the only way then to demonstrate the existence of competition is to compare in a quantitative manner the realized and fundamental niches of suspected competitors.

SUMMARY

During winter the bark-foraging guild of birds in deciduous woodlands of central Illinois consists of the Red-headed Woodpecker, the Red-bellied Woodpecker, the Downy Woodpecker, the White-breasted Nuthatch and the Brown Creeper. Previous work suggested that the aggressive Red-headed Woodpecker greatly influenced the organization of this guild. Red-headed Woodpeckers store acorns and corn in bark crevices during years with good mast crops and defend surrounding territory against all intruders. We removed the Red-headed Woodpeckers from a 5.9-ha woodlot and observed the response of other guild members. Red-bellied Woodpeckers and nuthatches, which had previously been excluded by Red-headed Woodpeckers, entered the experimental area but not the control area where Red-headed Woodpeckers remained. Downy Woodpeckers foraged higher in the trees than they had previously in the experimental area, and higher than in the control area. During the following winter, when Red-headed Woodpeckers were absent, subordinate species used the experimental area in a similar manner.

A graphic model was developed to explore the relationships among competition, niche breadth, and population density. Our analysis suggested that subordinates should broaden resource exploitation when a dominant species is added to the community if the population is not limited along that particular resource dimension. In contrast, if the population is limited along that dimension, the subordinate species should decrease its niche breadth. Our data showed both trends: Red-bellied Woodpeckers were restricted in horizontal space in the presence of Red-headed Woodpeckers, but Downy Woodpeckers increased their niche breadth along several dimensions.

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