COMPARATIVE FORAGING ECOLOGY OF DOWNY AND HAIRY WOODPECKERS (AVES: PICIDAE)

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ABSTRACT.—Information on the comparative ecology indicates little interspecific competition in areas of sympatry between the Hairy (*Picoides villosus*) and Downy (*P. pubescens*) woodpeckers. Preferences for certain tree species for foraging, the use of foraging stations of particular sizes, and the use of different foraging techniques, are compared for the two species. In the pine forests of the Bahama Islands, in the absence of the Downy Woodpecker, females of the Hairy are found in that part of the niche occupied by the Downy in areas of sympatry, probably as a result of limited food resources.

It is widely accepted that two species of animals cannot occupy the same area unless they differ ecologically. The foraging ecology and behavior of several North American woodpeckers has been studied (Austin 1976; Bent 1939; Bonner 1980; Connor 1979, 1980, 1981; Connor and Crawford 1974; Cruz and Johnston 1984; Gamboa et al. 1976; Jackson 1970; Kilham 1965, 1970, 1983; Kisiel 1972; Koch et al. 1970; Lawrence 1967; Ligon 1968a, 1968b; Lima 1983, 1984; Otvos 1967; Ouellet 1977; Peters and Grubb 1983; Rand 1952; Selander 1965, 1966; Short 1970, 1982; Smith 1971, 1973; Travis 1977; Villard and Beninger 1993; Wallace 1974; Williams 1975, 1980; Williams and Batzli 1979a) but few works have dealt with sympatric species with an extensive distribution. In this paper I am seeking to verify how two species, the Hairy (*Picoides villosus*) and Downy (*P. pubescens*) woodpeckers (hence Hairy (ies) or Downy (ies), sympatric over a large portion of their respective range (A.O.U. 1983) and with similar color patterns but with marked differences in their overall body size and other mensural characters, can occupy the same area by comparing aspects of their foraging ecology.

METHODS

The main study area was located at Mont Saint-Hilaire, in southwestern Quebec, Canada, at the Gault Estate of McGill University (45° 33'N, 73° 10'W; over 900 ha), 35 km east of Montreal, and in adjacent regions at various times from 1964 to 1970. The flora and its ecological aspects have been described by Maycock (1961). Additional data were collected in similar areas in the Great Lakes-St. Lawrence Forest Region (Rowe 1972), in other parts of Quebec, and in Ontario from 1966 to 1990. In March and April 1968, observations were made in Washington, Oregon, California, New Mexico, and Arizona. In March 1966, data on the Hairy were obtained in the pine forests of New Providence and Great Abaco islands, in the Bahama Islands, where the Downy is not known to occur (A.O.U. 1983). Other data were gathered in the Boreal Forest Region (Rowe 1972) and its southern ecotone in the Upper St. Maurice River and Abitibi regions of Quebec in 1967, 1968, and 1972.

Observations were made intensively from mid-September 1964 to mid-November 1965, from May through July 1966, and irregularly thereafter until December 1990. Data were recorded variously from daybreak to sunset, under various weather conditions. Birds were followed until they disappeared when observed foraging or when seen moving on tree trunks or branches. Each observation was recorded as one sighting along with the activities of the bird, provided that the activity lasted more than 30 seconds. Binoculars were used when necessary.

The following data were recorded: Species of woodpecker, sex, locality, date, number and species of trees on which the activities were taking place, diameter of trunks or branches (number of times on each), height of trees, foraging activities (gleaning, pecking, excavating, flycatching, sap-drinking), behavioral activities, foraging heights, time spent on trees or branches, time of day, and general climatic conditions.

The frequencies of occurrence in each category were tested by means of the G statistic (Sokal and Rohlf 1981) and the significance level accepted is $P < 0.01$.

RESULTS

Tree selection.—The Hairy occurs throughout most of the forested parts of North and Central America (A.O.U. 1983) whereas the distribution of the Downy ends near the U.S.A.- Mexico border (A.O.U. 1983) but the habitat preferences of each species vary geographically.

At Mont Saint-Hilaire and in the adjacent areas in the Great Lakes–St. Lawrence Forest Region (Rowe 1972) the Hairy is well-distributed in wooded areas of various sizes and ages at all times of the year. It displays a marked preference for American Beech (*Fagus grandifolia*) and other hardwood species (Table 1). The fact that American Elm (*Ulmus americana*) rates highly on the list appears to be resulting from the serious damage caused to that tree by the Dutch elm disease during the 1960's and 1970's (Kilham 1973). Trees with a coarse bark like most maples (*Acer* spp.) and oaks (*Quercus* spp.) provide a more extensive foraging surface than species with a smooth bark like beech. Consequently, the former species would be expected to be selected first by foraging birds (Jackson 1979, Travis 1977) but those species rank below beech (Table 1). The intersexual difference in tree species is highly significant (Table 1), females favouring dead elms (X^2=18.545; d.f.=6; G=146.918;P<0.005).

Observations in the boreal forest of Quebec and Ontario (Table 2), from May through August, show that Trembling Aspen (*Populus tremuloides*) and other aspens (*Populus* spp.), as well as birches (*Betula* spp.) are used more frequently by the Hairy than conifers. The Hairy is rare and the Downy is nearly absent in extensive stands of Jack Pine (*Pinus banksiana*). Dead and burnt stumps are also used frequently. There is no significant intersexual difference in the selection of tree species for foraging in the boreal forest (X^2=13.277; d.f.= 3; G= 4.683, P> 0.01).

In the humid coastal forests of Washington State, in March 1968, no intersexual difference was observed in the tree species selected in spite of a small sample (X^2=9.201; d.f.= 2; G=0.830, $\underline{P}$> 0.01). Hairy show a preference for conifers and large deciduous trees, whereas alders (*Alnus* spp.) and willows (*Salix* spp.) are used less frequently. Elsewhere in the interior of the western part of the range (California, New Mexico, and Arizona), in the montane woodland, no significant intersexual difference in tree selection was noted during March and April 1968 (Table 4; $\underline{X}^2$=13.277; d.f.= 4; G= 1.551, $\underline{P}$> 0.01), both sexes using pines and oaks more frequently than any other species. In certain situations, mainly along rivers, willows, aspens, and cottonwoods (*Populus* spp.) also were used.

In the Bahama Islands, only six sightings were recorded on deciduous trees in March 1966 (*Casuarina* sp.: 4 for males and 2 for females) from a total of 1,991 sightings (1,055 for males and 936 for females). All the other sightings were registered on Caribbean Pines (*Pinus caribaea*). The Hairy is thus specific to pines on the Bahama Islands, considering that a few deciduous trees are found in pine stands, particularly at edges and in areas of regeneration. It is worth noting that a live, hollow *Casuarina* sp. was used for nesting at the edge of a golf course where almost all pines had been removed.

In the Great Lakes-St. Lawrence Forest Region of eastern Canada (Rowe 1972), mainly in the relatively undisturbed forest stands of Mont Saint-Hilaire, Downy

Woodpeckers showed a marked preference for beech and dead elms particularly in fall and winter (Table 1). Sugar Maple (*Acer saccharum*) comes third whereas oaks and pines are used less frequently. Other deciduous species like aspens, alders, willows, serviceberries (*Amelanchier* spp.) etc., also are used. It is somewhat surprising to find that beech is used most frequently in this type of forest because its relatively smooth bark does not appear to provide as large a foraging surface area as the other species with rougher bark but its softer bark may maintain a higher density of prey. Beech trees used by the Downy usually have smaller diameters (D.B.H.) than those exploited by the Hairy (Table 1). However, the numerous small knot holes, cracks, and shallow crevices of the bark may yield a high percentage of prey more attractive to the Downy than the prey found on other trees and those may be easier to obtain on beech than on rough-barked species (Jackson 1979, Travis 1977). This situation is similar to that of the Hairy which forages on larger trees. However, it appears that these woodpeckers search for different prey (Beal 1911; Kroll et al. 1979, 1980; McAtee 1911; Petit et al. 1988; Williams and Batzli 1979b). A significant intersexual difference was found in the frequency of trees used for foraging (X^2=19.545; d.f.= 6; G=200.1; P< 0.005). This difference can be accounted for partly by the fact that females (13%) were observed more frequently than males (9.5%) in alders and willows and that males (8.9%) forage more frequently in aspens than females (5.3%). In that part of the range, significant interspecific differences were found (X^2= 18.545; d.f.= 6; G= 3,362.059; P<0.005). The Hairy uses beech, maple, and pine more often than the Downy . However, the latter made more frequent use of dead elms (particularly during winter months), aspens, willows, and alders than its larger congener. American Beech is thus selected more frequently (Table 1; 45.1%) by the Hairy than other tree species in this forest region.

In the coniferous forest, no significant intersexual difference in the selection of tree species by the Downy was detected (Table 2; X^2 = 13.277; d.f. = 4; G = 6.949, P > 0.01). Birches rank first (31.9%) and are followed by aspens (27%) and willows and alders (17.3%). Foraging on other trees amounts to 13.7 per cent on conifers and 10.2 per cent on dead and burnt trees. However, the interspecific difference in tree species is highly significant (Table 2; X^2 = 14.860; d.f. = 4; G = 1,332.953; P < 0.005), the primary difference being that Hairies use aspens and dead or burnt trees more frequently than Downies which were observed more frequently on birches, alders, and willows.

In the Pacific Rain Forest Region of Washington State, the proportions of trees selected by male Downies do not differ significantly from those used by females (Table 3; X^2 = 9.210; d.f. = 2; G = 0.600; P > 0.01) and these birds were observed foraging primarily on alders and willows as well as on other large deciduous species but rarely on conifers. The interspecific difference is highly significant (Table 3; X^2 = 10.597; d.f. = 2; G = 52.138; P < 0.005) although both birds frequently forage on large deciduous trees (*P. villosus* = 37.0%, *P. pubescens* = 46.1%).

In the interior of the western part of its range the Downy (California, New Mexico, and Arizona), the intersexual difference tree choice, primarily in the montane woodland, was found to be non-significant (Table 4; X^2 = 13.277; d.f. = 4; G = 3.397; P >0.01). Although both sexes were found to forage frequently on large deciduous trees, softwood deciduous trees were chosen over hardwood species. A significant interspecific difference in tree species shows that Hairies select more frequently pines and oaks and that Downies forage mainly on softwood deciduous species like alders, willows, aspens, and cottonwood (Table 4; X^2 = 14.860; d.f. = 4; G = 96.124; P < 0.005).

Foraging height.—Foraging height is highly variable in woodpeckers as shown by Conner (1979, 1980), Jackson (1970), and Selander (1965, 1966). During my field studies I never found a satisfactory way of recording foraging heights other than registering the height at which a bird starts and the height at which the activity stops, or where the bird leaves the tree. This aspect of the foraging ecology has therefore not been treated here for this reason.

Foraging stations.—The selection of foraging stations or sites in the Hairy and Downy woodpeckers has been discussed (Grubb 1975, 1977, 1978; Jackson 1970, 1979; Kilham 1961, 1965, 1970, 1973, 1983; Kisiel 1972; Lawrence 1967) and for other species (Ligon 1968a, 1968b; Selander 1965, 1966; Villard and Beninger 1993; Wallace 1974; Williams 1975, 1980). Temporal, sexual, and spatial differences were found between sympatric species and these differences are in general agreement with the following results.

Choice of foraging stations.—In the Hairy (Table 5) both sexes forage on the trunk as well as on limbs but males use trunks more frequently than females and females have been observed more frequently on branches. Both sexes forage occasionally on the ground or on trunks or branches lying on the ground. The difference between the observations of females foraging on branches compared to those against trunks is not well marked but the choice of foraging stations by females is significantly different from that of males (Table 5; $X^2 = 10.597$; d.f. = 5; G = 676.136; $P < 0.005$).

In the Downy the intersexual difference is highly significant (Table 5; $X^2 = 10.597$; d.f. = 2; G = 341.365; $P < 0.005$). Females forage more often on branches than males whereas the latter forage also on branches and trunks, and females go somewhat more frequently to the ground than males. The interspecific difference in the choice of foraging stations selected by the Hairy and Downy woodpeckers is highly significant (Table 5; $X^2 = 10.597$; d.f. = 2; G = 812.655; $P < 0.005$). Hairies are found more frequently on trunks than of branches and Downies more frequently on branches.

Live versus dead trees.—Jackson (1970) and Kisiel (1972) found differences in the choice of trees used for foraging. My data, collected mainly in the Great Lakes-St. Lawrence Forest Region (Table 6), show no significant intersexual difference in the choice of live versus dead trees, particularly in the Hairy (50.9% - 49.1%) but females of the Downy (47.3% - 52.7%) show a slight preference for dead trees even in summer. On the other hand, Hairies do not show any preference for the type of trees used for foraging throughout the year (Table 6; $X^2 = 6.635$; d.f. = 1; G = 4.337; $P > 0.01$). Downies display a preference during the summer months for live trees and for dead trees during the rest of the year (Table 6; $\underline{X}^2 = 6.635$; d.f. = 1; G = 7.629; $\underline{P} < 0.01$). However, no significant interspecific difference appears in the choice of the types of trees selected for foraging (Table 6; $X^2 = 6.635$; d.f. = 1; G = 5.839; $P > 0.01$). The condition of the trees appears to have significance only with the Downy , particularly in winter when dead elms were selected (versus live trees in summer) more frequently. This factor was of special importance following the massive die off of elms in the late 1960s and early 1970s (Kilham 1961, 1973).

Diameter of foraging station.—Intersexual selection takes place in the choice of the foraging substratum in both woodpeckers, mainly with regards to the species of trees used and certain parts of the trees (trunk versus branches).

Diameter of trunks and branches – Eastern Canada.—In the Great Lakes-St. Lawrence Forest and Boreal Forest regions (Table 7) no significant trend in the size selection of foraging stations has been found. Females of the Hairy tend to use more frequently than males trunks larger than 30 cm in diameter (DBH) whereas males spend more time on trees with a DBH of 10-20 cm (Table 7; $X^2 = 16.750$; d.f. = 5; G = 677.802; $P < 0.005$).

In the Downy both sexes forage more frequently on trunks with a DBH of 10 cm or less than Hairies but females use those more often than males, which tend to forage more frequently on trunks with a DBH greater than 10 cm, while they use more often those with a DBH in the 10-20 cm class. Intersexual differences in the use of trees of different sizes are highly significant (Table 7; $X^2 = 16.750$; d.f. = 5; G = 333.910; $P < 0.005$).

Interspecific differences are more striking, the Downy foraging significantly more frequently on trunks with a DBH of less than 10 cm whereas the Hairy has been observed more often on trees with a DBH of more than 20 cm, although some overlap occurs in the 10-20 cm DBH class. The frequencies obtained for each species on each trunk class are significantly different (Table 7; $X^2 = 16.750$; d.f. = 5; G = 15,580.546; $P < 0.005$). These results confirm a well-marked niche partitioning between the two species in their selection of tree trunks for foraging.

Hairies show no significant intersexual difference, both sexes using more frequently (± 70%) branches with a diameter of less than 10 cm and the least (11.8%) branches less than 5 cm in diameter (Table 8; $X^2 = 9.210$; d.f. = 3; G = 1.220; $P > 0.01$). Males and females Downies display similar foraging frequencies on branches with a diameter less than 10 cm but males forage significantly more often than females (7.1 % / 3.3%) on branches with a diameter greater than 15 cm which appear to account for the difference observed in the intersexual use of foraging sites (Table 8; $X^2 = 12.838$; d.f. = 3; G = 64.110; $P < 0.005$). Interspecific frequencies in the use of branch sizes are significantly different (Table 8; $X^2 = 12.838$; d.f. = 3; G = 5,115.945; $P < 0.005$). Hairies select more frequently larger branches than Downies with little interspecific overlap in the use of branches particularly those exceeding 15 cm in diameter. As well, each species and males and females Downies use a well-defined range of branch size for foraging.

Diameter of trunks and branches – Pacific Rain Forest.—No significant intersexual difference in the selection of a particular size of foraging medium was observed in both woodpeckers in this life region (Table 9; $X^2 = 15.086$; d. f. = 5; G = 4.456; $P > 0.01$). However, the combined data show a significant interspecific difference (Table 9; $X^2 = 16.750$; d. f. = 5; G = 53.757; $P < 0.005$), Hairies foraging more frequently on trunks and branches with a diameter greater than 20 cm. Downies were seen more frequently on branches and trunks with a diameter of less than 20 cm. The fact that Hairies obtain a high percentage in the 5 cm or less class can be explained by their presence on the smaller branches of the large conifers of this life region.

Diameter of trunks and branches – Western Montane Woodland.—In this ecological region the two species forage on different trees (Table 4): conifers and oaks for Hairies and willows, alders, and cottonwood for Downies. No intersexual differences in the use of foraging media were found in either species (Table 10; $X^2 = 15.086$; d. f. = 5; *P. villosus*: G = 8.703; *P. pubescens*: G = 8.703; $P > 0.01$) but the difference is significant when intersexual data are combined and compared for each species (Table 10; $X^2 = 16.750$; d.f. = 5; G = 159.831; $P < 0.005$). The Hairy selects larger foraging sites than its congener and niche partitioning is expressed in two ways: selection of foraging sites of different sizes by each species and use of different tree species for foraging.

Diameter of trunks and branches – Bahama Islands.—Observations on the intersexual use of foraging sites of different sizes by Hairies in the pine forests of the Bahama Islands show highly significant intersexual differences (Table 11; $X^2 = 14.860$; d.f. = 4; G = 1,224.77; $P < 0.005$). Males forage more frequently on trees with a DBH larger than 10 cm whereas females were observed more often on smaller trunks and branches, although males do not avoid the latter (17.6%). It thus appears that females Hairies occupy here a niche which is left unoccupied in this part of its range in the absence of the Downy. It has little or no interactions with the West Indian (*Melanerpes superciliaris*) which occupies different habitats in the Bahamas.

Foraging activities.—Kilham (1965) and Jackson (1970) described activities related to foraging for both Hairy and Downy woodpeckers. I have used a slightly different terminology in describing and comparing the foraging activities of both birds. Based on my field observations the foraging activities of these birds can be divided into three main groups and two marginal categories:

GLEANING – refers to any type of foraging taking place at the surface of the bark or in crevices, with the exclusion of the activities listed below. It comprises "percussion", "peering and poking", and "scanning from a distance" as described by Kilham (1965). It includes also the movements of the birds on the surface of the medium in search of food and the actual taking of prey at the surface.

PECKING – combines the "pecking" and "scaling" of Kilham (1965) and the "scaling" of Jackson (1970) and consists in the removal of bits of bark to reach preys by means of a few blows of the bill or by placing the bill under or on the side of poorly secured pieces of bark. This heading comprises the two categories of Kilham (1965) because "pecking", contrary to Jackson's definition (1970), is a more comprehensive and less specialized term than "scaling" to describe a variety of foraging activities. As well, I found it difficult to distinguish between "scaling" and "pecking" (*sensu* Kilham 1965) unless observations were made at close range.

EXCAVATING – is a common activity in both species and excludes all excavating activities associated with nesting and is restricted to foraging for food. It consists in the extraction of prey in the bark, under the bark on the cambium, or in the wood of a trunk or branch, live or dead, by actually digging into those substances with the bill. Depths of more than 5 cm in digging for wood-boring larvae have been occasionally recorded in the activities of the Hairy . In this manner, sizeable chunks or splinters of wood are removed by means of sharp blows of the bill and then seized to be tossed aside if they have not already fallen off to the ground.

FLYCATCHING – is rare and was seldom recorded but was more frequent in the Downy . It was observed mainly on warm calm days and is done in two ways: by sitting on a dead limb, in the open, and by waiting for an insect to fly by and capturing it in a typical flycatcher fashion, including bill-snapping; by capturing flying insects on the wing when the bird is engaged in foraging in some other fashion.

SAP-DRINKING – is unusual for these woodpeckers and was observed only in the Downy at Mont St. Hilaire, Quebec, during May, at sap-holes excavated by the Yellow-bellied Sapsucker (*Sphyrapicus varius*) in maples and aspens. Few encounters were recorded between the two species. This behavior has not been reported previously for the Downy but Kilham (1965: 140-141) observed it in the Hairy .

Foraging activities – Eastern Canada.—A highly significant intersexual difference was found in the Hairy (Table 12; $X^2 = 12.838$; d.f. = 3; G = 15.721; $P < 0.005$). Males "excavate" more frequently than females which in turn "peck" more often than males. Little intersexual difference was observed in "gleaning" which is not a frequent activity in this species. "Flycatching" is not usual either but was observed more frequently in males than females and coincides with warm and windless days. During the nesting season, the relative frequencies of foraging activities shift and most of the food is obtained, in both sexes, by "excavating". "Gleaning" decreases and "flycatching" remains unimportant at this time of the year but the intersexual differences in these activities are significant (Table 12; $X^2 = 12.838$; d.f. = 3; G = 66.806; $P < 0.005$).

In the Downy intersexual differences in foraging are significant (Table 12; $X^2 = 14.860$; d.f. = 4; G = 25.951; $P < 0.005$) throughout the year. Males obtain higher frequencies while "gleaning" and "excavating" whereas females have been observed "pecking" and "flycatching" more often. "Sap-drinking" is a marginal and opportunistic activity (Foster and Tate 1966) that has probably arisen in areas of sympatry between the Downy and the Yellow-bellied Sapsucker and little intersexual difference was observed in this foraging activity. During the nesting season, the intersexual difference in the overall modes of foraging remains highly significant (Table 12; $X^2 = 12.838$; d.f. = 3; G = 20.177;

$P < 0.005$) and "pecking" increases whereas "gleaning" diminishes when compared to the annual values.

The modes of foraging of both species are different throughout the year (Table 12; $X^2 = 14.860$; d.f. = 4; G = 18,993.164 ; $P < 0.005$) and during the nesting season (Table 12; $X^2 = 12.838$; d. f. = 3; G = 10,479.755 ; $P < 0.005$). The Hairy can thus be characterized by its "excavating" activity in foraging while the Downy is concentrating primarily on "gleaning." Overlap occurs between the two species in "pecking" but the diameter of the foraging station is different as shown earlier. This overlap is considerably reduced during the nesting season because the Hairy then spends more time "excavating." Competition between the two species is thus reduced to a minimum during a critical period in the life of those birds. "Sap-drinking" by the Downy was not recorded during the nesting season probably because little sap runs at the holes in the bark at that time of the year. "Flycatching" is more frequent in the Downy during the breeding season because it is unlikely that this activity could take place at other times of the year unless the weather becomes warm enough to allow insects to fly.

Foraging activities – Bahama Islands.—The birds found in the Bahama Islands occur in the coniferous forests of Caribbean Pines on which they forage almost exclusively. A significant intersexual difference was found in the modes of foraging (Table 12; $X^2 = 10.587$; d. f. = 2; G = 13.558 ; $P < 0.005$). Males "peck" and "excavate" more frequently than females which "glean" more often than males.

Foraging activities – Pacific Rain Forest.—The Hairy and Downy woodpeckers use different species of trees for foraging in this life region but no intersexual difference has been found in their mode of foraging (Table 12; $X^2 = 9.270$; d. f. = 2; G = 0.400 ; $P > 0.01$). Males Hairies "excavate" and "peck" more often than females but the latter "glean" more frequently. In the Downy the situation is similar; males "excavate" and "peck" more than females, while females "excavate' more than males. The species in general however "gleans" and "pecks" more than "excavates," while the Hairy "excavates" more than it "gleans" and "pecks" (Table 12; $X^2 = 10.597$; d. f. = 2; G = 19.038 ; $P < 0.005$). In spite of the overlap in "pecking", competition between the two species is attenuated by the fact that each species forages to a great extent on different species of trees.

Foraging activities – Western Montane Woodland.—In this diversified ecological region no intersexual difference was observed in the Hairy (Table 12; $X^2 = 9.210$; d. f. = 2; G = 0.803 ; $P > 0.01$) or the Downy (Table 12; $X^2 = 9.210$; d. f. = 2; G = 3.573 ; $P > 0.01$) but a highly significant interspecific difference has been observed (Table 12; $X^2 = 10.597$; d. f. = 2; G = 27.227 ; $P < 0.005$). For the Hairy the "excavating" frequencies are significantly higher than those obtained for the Downy which was recorded "gleaning" more frequently. Although there is an interspecific overlap in the absolute frequencies of "pecking," the two woodpeckers forage on different tree species in that part of the range and each bird selects foraging substrata of different sizes. Thus intraspecific competition is reduced and allows both species to coexist in the same geographic area.

In summary, these two woodpeckers have evolved complex foraging strategies that allow them to coexist in the same habitat. The Hairy selects tree species that are different from those used by the Downy with regard to their size and the type of foraging substratum. The Hairy forages more often on substrata with a larger diameter than those on which the Downy is found. The mode of foraging of each bird is different, the Hairy was found "excavating" more often than the Downy which "gleans" more frequently than its congener. The overlap in "pecking" is reduced by the use of different foraging sites. In the absence of the Downy on the Bahama Islands, the Hairy occupies those parts of the trees on which its smaller congener is expected to be found and the foraging behavior of females resembles that of the Downy, as observed in areas of sympatry, as well as by making more frequent use of foraging techniques peculiar to the Downy.

DISCUSSION

Competition between sympatric species occupying a similar habitat has been the object of a number of publications which have provided useful compilations of data and various interpretations (Cody 1969, 1974; Lack 1967a, 1967b, 1968, 1971; MacArthur 1958, 1972; MacArthur and Levins 1967; Mayr 1970; Wynne-Edwards 1962). In order to coexist congeneric species have evolved strategies which allow them to occupy individual 'niches'.

Hairy and Downy woodpeckers, two similarly color-patterned congeneric species, sympatric over most of their respective range, have evolved their own strategies to coexist sympatrically, and, in certain parts of their range, to coexist with other congeneric species as well. Each woodpecker favors one type of tree over another, and that differences in 'niche' choice are important in areas where both species occupy similar habitats. In those areas the niche preferences of each species have been found to be different in the choice of trees used for foraging. Selection then occurs at two levels: 1) in the choice of a distinctive general habitat by each species, and, 2) in the choice of a specific niche by each species where both species occur sympatrically in similar habitats.

The Hairy selects more frequently tree trunks for foraging and the Downy, branches. This in itself could be considered a significant partitioning of the niche sufficient to permit the coexistence of two congeneric species, all year, in the same habitat. However, my results, contrary to those of Jackson (1970) and Kisiel (1972) do not indicate that live trees are favored over dead trees by one bird when compared with the other, except for females of the Downy, which favored dead elms during the late 1960s and early 1970 following the mass killing of those trees by the Dutch elm disease (Kilham 1961, 1973). A selection in favor of dead trees, which, theoretically, should provide more insect resources than live or live-shelled trees, would, however, be expected. But the bark of mature trees such as American Beech and other favored species may provide a more abundant or diversified surface or sub-surface insect fauna than dead trees because of its tender bark. In dead trees more energy may be required to reach the deep woodboring larvae. It may thus be more advantageous to these two woodpeckers, especially in winter when the subsurface parts are frozen hard, to search for insects on the surface as with the Downy or just below the surface of the bark like the Hairy , using foraging techniques that require a relatively lesser expenditure of energy compared with the excavating deeply in a hard substratum. In the areas of sympatry the two species have evolved additional foraging strategies to reduce interspecific competition. The selection by each species of foraging substrata of different diameters appears to be very important. This fact is reinforced by the situation on the Bahama Island where the Hairy occurs in the absence of the Downy. In the pine forests of the islands, both sexes tend to forage on smaller tree trunks and branches than what would be expected in similar habitats in areas of sympatry with the Downy, and females of the Hairy, using foraging stations selected by the Downy in eastern North America.

The divergence in the choice of foraging stations of different sizes by the two birds is amplified by the differences in their respective modes of foraging and adds to the information provided by Lack (1971) on the selection of a particular niche by sympatric ecologically similar species, the mode of foraging peculiar to each species, and the reduction in the competition for food resources.

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TABLE 1

COMPARATIVE NUMBER OF SIGHTINGS THROUGHOUT THE YEAR, BY SPECIES AND SEX, ON TREES USED FOR FORAGING IN THE GREAT LAKES – ST. LAWRENCE FOREST REGION OF CANADA, 1965-1990.

	Hairy Woodpecker (23,284)*		Downy Woodpecker (18,467)*	
TREE SPECIES	MALES	FEMALES	MALES	FEMALES
Fagus grandifolia	5,647	4,868	3,216	3,001
Acer saccharum and other *Acer* spp.	3,361	2,943	1,750	1,194
*Ulmus americana***	1,974	2,359	2,819	2,744
Quercus rubra and other *Quercus* spp.	237	201	177	139
Populus spp.	195	116	872	461
Pinus spp.	148	223	18	14
Others, including *Salix* and *Alnus* spp.	453	563	934	1,128
Total	12,015	11,269	9,786	8,681

* Total number of sightings. A sighting is an observation lasting more than 30 sec.

** Mostly dead trees.

TABLE 2

COMPARATIVE NUMBER OF SIGHTINGS THROUGHOUT THE YEAR, BY SPECIES AND SEX, ON TREES USED FOR FORAGING IN THE BOREAL FOREST REGION OF QUEBEC AND ONTARIO, 1965-1990.

	Hairy Woodpecker (223)*		Downy Woodpecker (226)*	
TREE SPECIES	MALES	FEMALES	MALES	FEMALES
Populus tremuloides	47	42	28	33
Betula spp.	27	37	38	34
Picea spp., *Abies balsamea*	8	11	12	19
Salix and *Alnus* spp.	4	10	16	23
Dead and burnt trees	20	17	16	7
Total	106	117	110	116

* Total number of sightings.

TABLE 3

COMPARATIVE NUMBER OF SIGHTINGS, BY SPECIES AND SEX, ON TREES USED FOR FORAGING IN THE PACIFIC RAIN FOREST REGION OF WASHINGTON STATE, MARCH 1968.

	Hairy Woodpecker (73)*		Downy Woodpecker (89)*	
TREE SPECIES	MALES	FEMALES	MALES	FEMALES
Conifers	19	15	2	1
Large deciduous trees	13	14	18	23
Populus, Salix, and *Alnus* spp.	5	7	21	24
Total	37	36	41	48

* Total number of sightings.

TABLE 4

COMPARATIVE NUMBER OF SIGHTINGS THROUGHOUT THE YEAR, BY SPECIES AND SEX, ON TREES USED FOR FORAGING IN INTERIOR CALIFORNIA, NEW MEXICO, AND ARIZONA, APRIL 1968.

	Hairy Woodpecker (208)*		Downy Woodpecker (131)*	
TREE SPECIES	MALES	FEMALES	MALES	FEMALES
Pinus spp.	37	31	9	6
Quercus spp.	33	29	3	1
Other conifers	8	11	6	3
Other hardwood species	9	7	11	15
Populus, Salix, and *Alnus* spp.	20	23	37	40
Total	107	101	66	65

* Total number of sightings.

TABLE 5

NUMBER OF SIGHTINGS AND TYPES OF FORAGING STATIONS BY SPECIES AND SEX.

	Hairy Woodpecker (22,856)*		Downy Woodpecker (17,848)*	
FORAGING STATION	MALES	FEMALES	MALES	FEMALES
Tree trunks	7,764 (65.1)**	5,253 (48.1)	4,731 (49.4)	2,969 (35.9)
Branches	4,014 (33.6)	5,498 (50.3)	4,619 (48.3)	4,996 (60.4)
Ground	155 (1.3)	173 (1.6)	223 (2.3)	310 (3.7)
Total	11,933	10,923	9,573	8,275

* Total number of sightings.
** Percentage.

TABLE 6

SELECTION OF LIVE VERSUS DEAD TREES FOR FORAGING IN EASTERN CANADA (GREAT LAKES – ST. LAWRENCE FOREST REGION), 1965-1990.

	Hairy Woodpecker (9,684)*		Downy Woodpecker (6,729)*	
	DEAD TREES	LIVE TREES	DEAD TREES	LIVE TREES
May to October	2,308 (47.8%)	2,513 (52.1%)	1,891 (48.8%)	2,012 (51.6%)
November to April	2,431 (50.0%)	2,432 (50.0%)	1,273 (45.0%)	1,553 (55.0%)
All year	4,739 (48.9%)	4,945 (51.1%)	3,164 (47.0%)	3,565 (53.0%)

* Total number of sightings for both sexes.

TABLE 7

DIAMETER OF FORAGING STATIONS - TRUNKS, 1965-1990.

	Hairy Woodpecker (19,062)*		Downy Woodpecker (10,227)*	
DIAMETER OF TREE (DBH)	MALES	FEMALES	MALES	FEMALES
5 cm or less	146 (1.6%)	76 (0.8%)	1,812 (31.7%)	1,428 (31.7%)
6-10 cm	139 (1.5%)	299 (3.0%)	1,427 (24.9%)	1,728 (38.4%)
11-20 cm	1,131 (12.3%)	657 (6.7%)	880 (15.4%)	341 (7.6%)
21-30 cm	3,380 (42.0%)	4,149 (42.2%)	1,239 (21.6%)	851 (18.9%)
31-40 cm	3,002 (32.5%)	4,279 (43.5%)	169 (3.0%)	75 (1.7%)
40 cm or more	934 (10.1%)	368 (3.7%)	196 (3.4%)	81 (1.8%)
Total	9,232	9,830	5,723	4,504

* Total number of sightings.

TABLE 8

DIAMETER OF FORAGING STATIONS - BRANCHES, EASTERN CANADA, ALL YEAR, 1965-1990.

	Hairy Woodpecker (5,467)*		Downy Woodpecker (7,088)*	
DIAMETER OF BRANCHES	MALES	FEMALES	MALES	FEMALES
5 cm or less	294 (11.5%)	352 (12.1%)	1,495 (41.2%)	1,363 (39.4%)
6-10 cm	443 (17.4%)	533 (18.2%)	1,397 (38.5%)	1,460 (42.2%)
11-15 cm	612 (24.0%)	694 (23.8%)	477 (13.2%)	525 (15.2%)
16 cm or more	1,197 (47.0%)	1,342 (45.8%)	258 (7.1%)	113 (3.3%)

* Total number of sightings.

TABLE 9

DIAMETER OF FORAGING STATIONS - TRUNKS AND BRANCHES IN PACIFIC RAIN FOREST, 1968.

	Hairy Woodpecker (73)*		Downy Woodpecker (89)*	
DIAMETER	MALES	FEMALES	MALES	FEMALES
5 cm or less	3 (8.1%)	5 (13.9%)	11 (26.8%)	17 (35.5%)
6-10 cm	——	2 (5.6%)	9 (22.0%)	6 (12.5%)
11-20 cm	3 (8.1%)	2 (5.6%)	9 (22.0%)	11 (22.9%)
21-30 cm	8 (21.6%)	9 (25.0%)	8 (19.5%)	9 (18.8%)
31-40 cm	16 (43.2%)	11 (30.6%)	4 (9.8%)	3 (6.3%)
40 cm or more	7 (18.9%)	7 (19.4%)	——	2 (4.2%)

* Total number of sightings.

TABLE 10

DIAMETER OF FORAGING STATIONS – TRUNKS AND BRANCHES IN WESTERN MONTANE WOODLAND, 1968.

	Hairy Woodpecker (208)*		Downy Woodpecker (128)*	
DIAMETER	MALES	FEMALES	MALES	FEMALES
5 cm or less	15 (14.0%)	14 (13.9%)	20 (30.3%)	22 (35.5%)
6-10 cm	8 (7.5%)	14 (13.9%)	9 (13.6%)	9 (14.5%)
11-20 cm	10 (9.3%)	13 (12.9%)	16 (24.2%)	15 (24.2%)
21-30 cm	23 (21.5%)	30 (29.7%)	17 (25.8%)	14 (22.6%)
31-40 cm	36 (33.6%)	23 (22.8%)	4 (6.1%)	1 (1.6%)
40 cm or more	15 (14.0%)	7 (6.9%)	——	1 (1.6%)

* Total number of sightings.

TABLE 11

DIAMETER OF FORAGING STATIONS - TRUNKS AND BRANCHES USED BY HAIRY WOODPECKERS IN THE BAHAMA ISLANDS, 1965. NUMBER OF OBSERVATIONS, 1,982*.

DIAMETER	MALES	FEMALES
5 cm or less	185 (17.6%)	379 (40.7%)
6-10 cm	158 (15.0%)	232 (24.9%)
11-20 cm	279 (26.5%)	178 (19.1%)
21-30 cm	352 (33.5%)	115 (12.3%)
31 cm or more	77 (7.3%)	28 (3.0%)

* Total number of sightings.

...continued

TABLE 12

FORAGING ACTIVITIES BY REGION, SPECIES, AND SEX.

			Gleaning	Pecking	Excavating	Flycatching	Sap-drinking
Great Lakes–St. Lawrence Forest Region and boreal forest, all year.							
Hairy W.	M	(20,121)*	469 (4.3%)	4,409 (40.1%)	6,110 (55.6%)	3 (0.03%)	——
	F		418 (4.6%)	3,884 (42.5%)	4,827 (52.9%)	1 (0.01%)	——
Downy W.	M	(17,725)	4,818 (53.0%)	3,721 (40.9%)	442 (4.9%)	29 (0.30%)	81 (0.9%)
	F		4,533 (52.5%)	3,681 (42.6%)	304 (3.5%)	43 (0.60%)	73 (0.8%)
Great Lakes–St. Lawrence Forest Region, Mont St. Hilaire, Quebec, nesting season.							
Hairy W.	M	(5,895)	63 (2.0%)	642 (20.4%)	2,436 (77.5%)	2 (0.10%)	——
	F		84 (3.1%)	793 (28.7%)	1,874 (68.1%)	1 (0.04%)	——
Downy W.	M	(9,804)	2,343 (48.6%)	2,206 (45.7%)	211 (4.4%)	64 (1.30%)	——
	F		2,467 (49.5%)	2,314 (46.5%)	116 (2.3%)	83 (1.70%)	——
Bahama Islands, March.							
Hairy W.	M	(1,985)	472 (44.9%)	492 (46.8%)	87 (8.3%)	——	——
	F	481 (51.5%)	406 (43.5%)	47 (5.0%)	——	——	——
Pacific Rain Forest, March.							
Hairy W.	M	(71)	7 (19.4%)	10 (27.8%)	19 (52.8%)	——	——
	F	9 (25.7%)	9 (25.7%)	17 (48.6%)	——	——	——
Downy W.	M	(86)	16 (41.0%)	15 (38.5%)	8 (20.5%)	——	——
	F	22 (46.8%)	17 (36.2%)	8 (17.0%)	——	——	——
Western Montane Woodland, March and April.							
Hairy W.	M	(201)	27 (26.0%)	42 (40.4%)	35 (33.7%)	——	——
	F	30 (30.9%)	39 (40.2%)	63 (28.9%)	——	——	——
Downy W.	M	(123)	29 (47.5%)	23 (37.7%)	9 (20.5%)	——	——
	F	33 (53.2%)	26 (41.9%)	3 (4.8%)	——	——	——

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