DOCTORAL DISSERTATION SERIES

TITLE A Comparative Life History Study of the Downy and Hairy Woodpeckers (Dendrocopus Pubescens and Dendrocopus Villosus)

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A COMPARATIVE LIFE HISTORY STUDY

OF THE

DOWNY AND HAIRY WOODPECKERS

(*DENDROCOPOS PUBESCENS* AND *DENDROCOPOS VILLOSUS*)

by

Arthur E. Staebler

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in the
University of Michigan
1949

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Most of this research was done while I held the Edwin C. Hinsdale Fellowships (1940-1941 and 1941-42) and Edwin S. George Scholarships (1946-47 and 1947-48).

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Purpose of the Study

The presence of two or more very similar species of the same genus living side by side over part or all of their respective ranges offers very interesting material for study. The subjects of this study are two such species, the Downy and the Hairy Woodpeckers (*Dendrocopos pubescens* and *Dendrocopos villosus*).

There are several genera of birds in which two or more members of the genus are remarkably similar in both morphological characters and biology. Among the passerines, one may mention the genera *Hylocichla* and *Empidonax* as outstanding examples. The genus *Dendrocopos* is remarkable for its number of similar forms whose ranges overlap, although the morphological similarity of its members is perhaps not as close as that of the members of *Hylocichla* or *Empidonax*.

Among the sympatric species of *Dendrocopos*, two pairs of species are interesting. The color patterns of *D. villosus* and *D. pubescens* are very similar. The main difference between the two is that of size, and the range of *pubescens* is entirely within that of *villosus*. The color patterns of *D. major* and *D. minor* of Europe are similar, although the similarity of their color patterns is not as marked as in the case of the *villosus* - *pubescens* pair.

Sibling species have been defined by Mayr (1942:151) as morphologically similar and closely related sympatric species. The similarity between sibling species may be so close that specimens can be identified by taxonomic characters only with difficulty. For many years it was believed that *Pericrocotus brevirostris* was one species, but Mayr (1940) established the presence of two species, *P. brevirostris* and *P. ethologus*. These two species are identical

in size but possess minute and constant differences in their respective color patterns.

There are several examples of sibling species in which the color pattern is almost identical, but a difference in size exists between the members of each pair. Ramphastos, Myiarchus and Totanus may be mentioned. In the last named genus, however, Nichols (1923) has pointed out that the similarity between T. flavipes and T. melanoleuca is superficial and great differences exist in their skeletal features.

Because of the very similar color pattern of D. villosus and D. pubescens they are considered here as sibling species. D. major and D. minor, although sympatric, can hardly be regarded as sibling species because of the differences in their respective color patterns. It should be recalled that the term "sibling species" is merely a convenient label for an interesting species phenomenon and its limits cannot be well defined (Mayr, 1942:151).

I studied the Downy and Hairy Woodpeckers as living birds in the field in an attempt to learn something of the differences and similarities in their behavior and actions. These differences and similarities have been studied in an effort to determine their possible influences on the present and past biology of these two woodpeckers.

Description of Methods

In the course of this study as much time as possible was spent in field work. Field study was carried throughout the year and not limited to the nesting seasons. A pair of 6x prism binoculars were used during field observations. Field work was started in February, 1940, and carried on almost continuously until mid-July, 1942. Following a 4-year interruption because of the war, field work was resumed in July, 1946, and carried on intensively until August, 1947. Occasional observations have been made from August, 1947, through June, 1948.

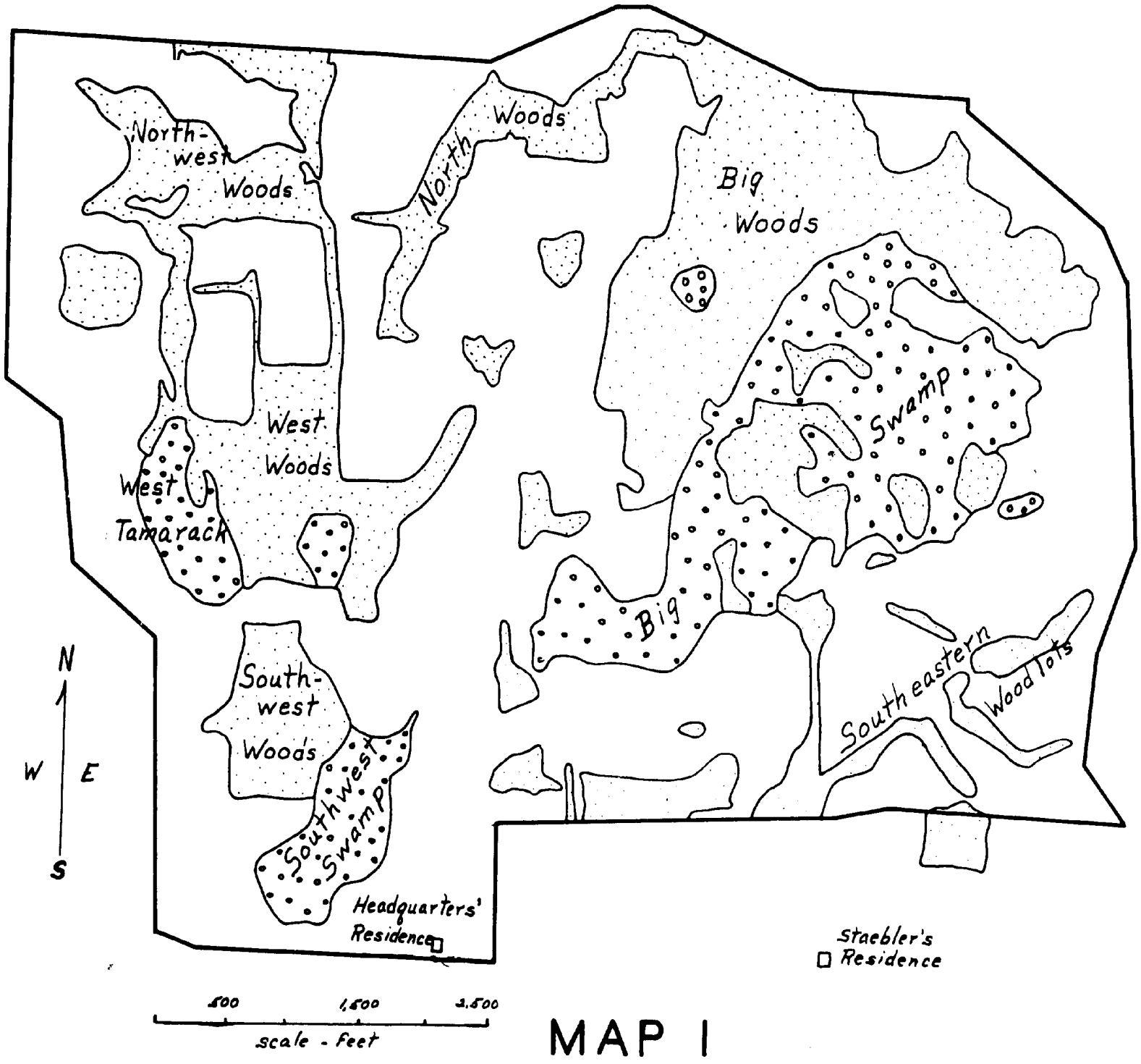
Most of the field work was done on the Edwin S. George Reserve, although some observations were made in an area 3 1/2 miles north of Ann Arbor in 1940, 1941, and 1942. The George Reserve is located in Livingston County, Michigan; it is 20 miles northwest of Ann Arbor and 10 miles south of Howell. The Reserve includes 1268 acres of rugged moraine and basin topography and for the most part hills and knobs alternate with kettle holes and basins. The altitude varies from 890 to 1,000 feet above sea level with about 25 per cent of the area below the 915 contour. About one-half of the area is grassy fields, one-fourth is hardwood forests and one-fourth is wooded swamplands. The Reserve is described in more detail by Rogers (1942). Unless otherwise stated, all observations mentioned in the text were made on the Reserve and all of the banding was done there. The names of the various woodlots and wooded swamps on the Reserve are shown on Map 1.

Explanation of Map 1

Names of Woodlots and Other Landmarks of the Edwin S. George Reserve

The oak-hickory areas are indicated by stippling.

The wooded swamplands, largely tamarack are indicated by open dots.


North-
west
Woods
North
Woods
Big
Woods
West
Woods
West
Tamarack
Swamp
Big
South-
west
Woods
Southwest
Swamp
Southeastern
Woodlots
N
W
E
S
Headquarters'
Residence
Staebler's
Residence
500
1,500
2,500
scale - Feet

MAP 1

Approximately 1,200 hours were spent in the field on 214 different days. The total number of hours and days in the field for each month are shown on Table 1.

The desirability of having the woodpeckers individually marked for field identification became apparent during the first months of the study. The following year (1941) two feeding stations were established on March 2. On March 16 the first woodpeckers were caught and marked; all were given Fish and Wildlife Service bands. The adult birds captured in the spring of 1941 were marked with colored feathers placed on the tail. The colored feathers were held in place by tying them with fine silk thread to a central tail feather and applying a bit of glue. White duck feathers dyed bright colors were used. These feathers worked very well for identification purposes until the birds started nesting. Apparently the feathers were broken off when the birds began going in and out of their nest holes.

Colored celluloid leg bands were first used when young Downys were banded in the nest in 1941. All adult and young Downys and Hairys captured after that were marked with colored celluloid leg bands. The Fish and Wildlife Service aluminum bands were incorporated in the formation of the many color combinations.

Colored bands on the legs of Hairys and Downys did not prove very satisfactory. The bands were difficult to see for several reasons. The habit of these two species of woodpeckers of clinging closely to their perch made it impossible even to see the legs in many instances. The tarsi of these birds are relatively short. The birds were rarely

TABLE 1

Monthly Totals of Hours and Field Trips

Month	Locality			
	George Reserve		Ann Arbor area	
	Hours	Trips	Hours	Trips
January	50	11		
February	70	14	5	1
March	140	23	15	3
April	105	19	50	14
May	185	35	50	10
June	165	29		
July	95	17		
August	40	7		
September	35	6		
October	60	8		
November	75	10		
December	50	9		
Totals	1070	186	120	28
Net Total	1190 hours		214 trips	

found at eye level but usually at a height considerably above the observer. It generally took fifteen minutes of close observation to identify an individual in the field; on a few rare occasions an hour's observation proved inadequate. As no other method that would mark each bird for life was known, the use of colored bands was continued for the balance of the study.

On Table 2 are listed the adult Downys that I banded and marked with colored celluloid leg bands. None of the young Downys color-banded as nestlings were ever seen again and therefore they have not been included in the table. On Table 3 are listed all of the Hairys that I banded with metal and colored celluloid bands.

The traps used to catch adult woodpeckers were wire cages constructed of hardware cloth. They were about 15 inches wide, 18 inches long and 10 inches high. A free swinging door was at one end. The traps were sprung manually by pulling a wire or string. Automatic traps were not used because of the large number of other birds, such as Black-capped Chickadees (Parus atricapillus), White-breasted Nuthatches (Sitta carolinensis), Tufted Titmice (Parus bicolor), and Bluejays (Cyanocitta cristata) that visited the traps almost constantly. By operating the traps manually, it was possible to catch only those birds that I desired. The traps were set on horizontal wooden platforms, slightly larger than the traps, and 4 1/2 to 5 feet above the ground on steel posts.

The locations of the traps on the Reserve are shown on Map 2. Not all of the traps were operated at the same time and only those in use were baited. Each trap was used during the season listed below.

TABLE 2

List of Adult Downy Woodpeckers Used in This Study

Male	Date of Banding	Trap of Capture	Right Leg	Left Leg
A	Nov. 16, 1941	1	metal	yellow
B	Nov. 21, 1941	3	metal	red
C	Nov. 23, 1941	4	metal	green
D	Feb. 1, 1942	3	yellow	metal
E	"	3	green	metal
F	"	3	red	metal
G	Feb. 8, 1942	2	red / green	metal
H	Feb. 19, 1942	1	red / yellow	metal
I	Dec. 19, 1946	9	red	metal / yellow
J	Jan. 11, 1947	6	metal	red / yellow
K	Jan. 23, 1947	7	red / metal	red
L	"	7	metal	green / yellow
M	"	7	metal / green	green
N	Jan. 27, 1947	6	metal	white
O	Feb. 8, 1947	7	metal	white / blue
P	Feb. 11, 1947	8	metal	green / white
Q	"	8	metal	green / blue
R	Feb. 12, 1947	10	white / metal	nothing
S	Feb. 13, 1947	6	red	yellow / metal
T	Mar. 10, 1947	10	metal / blue	green
U	Mar. 26, 1947	7	metal	yellow / blue
V	"	7	metal / green	white
W	Jan. 10, 1948	6	coral / green	metal / green
X	Feb. 2, 1948	6	red / coral	metal / green
Female				
A	Nov. 23, 1941	2	yellow	metal
B	"	1	red	metal
C	"	2	metal	red / green
D	Feb. 8, 1942	3	metal	red *
E	"	3	metal	red *
F	Feb. 19, 1942	1	metal	green
G	Dec. 11, 1946	6	red	red / metal
H	Dec. 19, 1946	9	metal	blue / green
I	Dec. 20, 1946	8	metal	blue
J	Jan. 2, 1947	8	nothing	metal / red
K	"	8	nothing	red / metal
L	Jan. 12, 1947	6	metal	yellow / green
M	Jan. 23, 1947	7	metal / yellow	yellow
N	"	7	metal	yellow / red
O	"	7	red	metal / red
P	"	7	red / metal	nothing
Q	Jan. 28, 1947	6	metal	blue / white
R	Feb. 8, 1947	7	metal	white / yellow
S	"	7	metal	blue / yellow
T	Feb. 12, 1947	10	metal / green	blue
U	"	10	metal / green	yellow
V	"	10	blue / metal	nothing
W	Mar. 19, 1947	6	metal / yellow	green
X	Nov. 18, 1947	6	coral	metal / green
Y	Nov. 20, 1947	6	yellow	metal / yellow
Z	"	6	green	metal / green
A'	Feb. 2, 1948	6	metal / red	yellow / red

* Inadvertently marked alike

Table 3

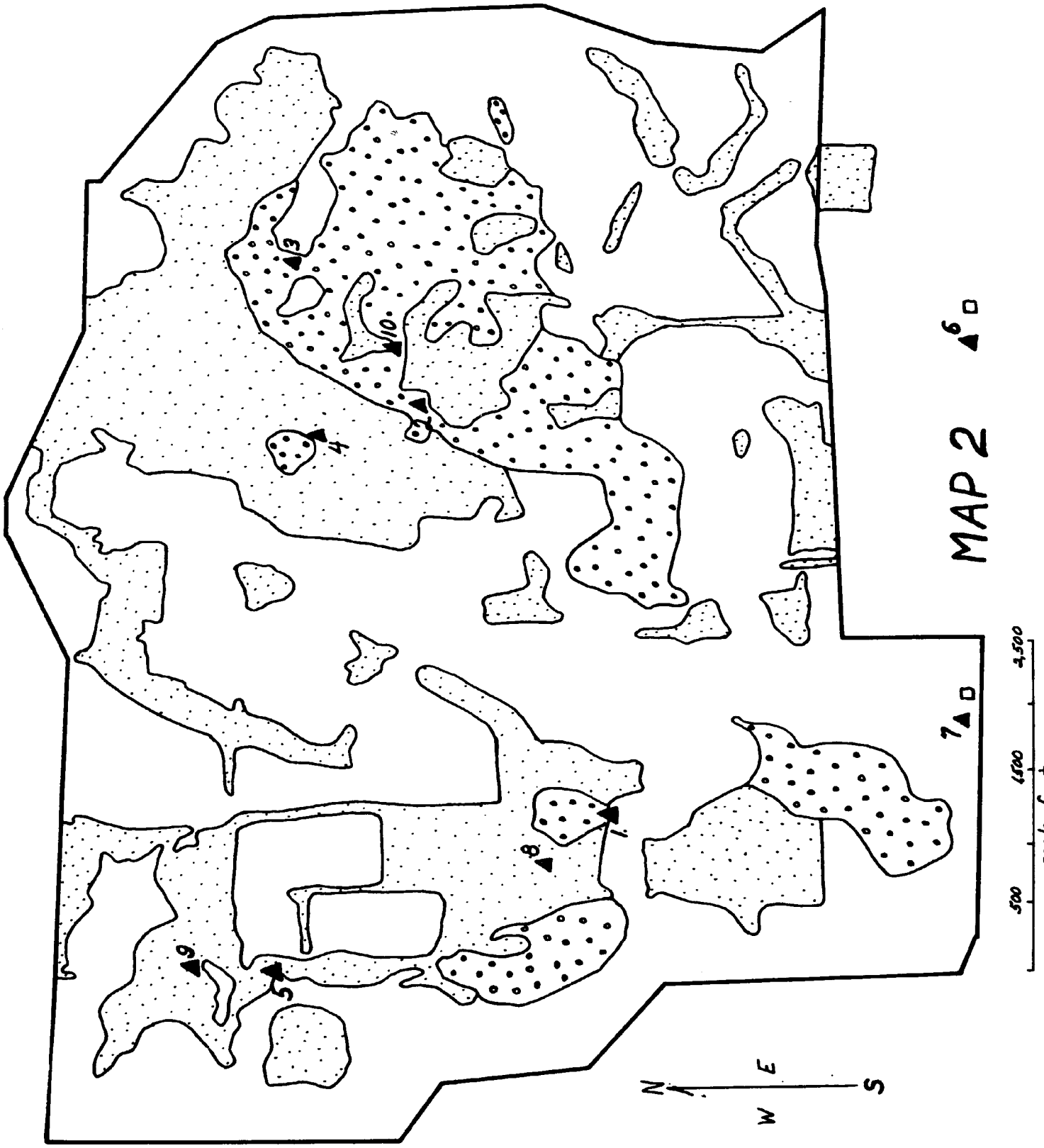
List of the Hairy Woodpeckers Used in This Study

Male	Date of Banding	Trap or Nest of Capture	Marking Combination	
			Right Leg	Left Leg
A	Jan. 29, 1947	Trap 9	metal	green
B	Mar. 10, 1947	Trap 10	metal	red / yellow
C	Mar. 28, 1947	Trap 7	metal	red
D (im)	June 6, 1947	Trap 3	nothing	metal / red
Female				
A	Nov. 16, 1941	Trap 1	metal	yellow
B	Jan. 29, 1947	Trap 9	yellow	metal
C	Feb. 16, 1947	Trap 6	red	metal
D	Feb. 2, 1948	Trap 6	red / yellow	metal
E (im)	June 6, 1947	Nest 3	metal / red	nothing
F (im)	"	Nest 3	metal / red	yellow

Explanation of Map 2

Location of Traps on the Edwin S. George Reserve

The traps are indicated by the solid triangles. Oak hickory woodlots are stippled, the forested swamplands, largely tamarack, are marked with open dots.


MAP 2
scale - feet
500
1500
2,500
N
E
S
W
1
2
3
4
5
6
7
8
9
10

Trap No. 1... Mar. 1941; Oct. 1941 through Feb. 1942

" 2... " " "

" 3... Oct. 1941 through Feb. 1942

" 4... " "

" 5... Oct. 1941 through Dec. 1941

" 6... in continuous operation from Nov. 1946

" 7... maintained as feeding station throughout period of study; trap there from Jan. 1947 through Mar. 1947

" 8... Oct. 1946 through Feb. 1947

" 9... " "

" 10... " "

The feeding station at the Headquarters House is maintained throughout the year. Downys and Hairys visit the suet there every month of the year and the feeding station is a center of activity of these birds. The station is at least 600 yards from the nearest wooded area of the Reserve and it is believe unlikely that this feeding station has had any appreciable influence on the normal activities of the birds. However, the establishment of numerous feeding stations with unlimited food supply on the Reserve was avoided. I feared that such a procedure might create an unnaturally large population.

I baited the traps in October and kept only relatively small amounts of suet in them until mid-December. During the period from mid-December to mid-February a constant supply of suet was kept at the traps. The suet was occasionally removed from the traps or

allowed to become eaten away by the birds so that the presence of that food supply would not be a possible factor in the formation of the nesting territories.

The numbers of Downys and Hairys banded each year are listed below. With the exception of the four adult Downys banded in the winter of 1940-1941, all birds were banded with colored celluloid bands in addition to the aluminum bands.

Adult Downy Woodpeckers banded during the winter season of:

	1940-41	1941-42	1946-47	1947-48	Totals
Male	2	8	14	2	26
Female	2	6	17	4	29

Young Downy Woodpeckers banded in the nest in:

	1941	1942	1947	Totals
Male	5	1	2	8
Female	6	1	2	9

Total Downys banded: 72

Adult Hairy Woodpeckers banded during the winter season of:

	1940-41	1941-42	1946-47	1947-48	Totals
Male	0	0	3	0	3
Female	0	1	2	1	4

Young Hairy Woodpeckers banded in the nest in:

	1941	1942	1947	Totals
Male	0	0	1	1
Female	0	0	2	2

Total Hairys banded: 10

Plan of Work

The study has been centered on the Downy and Hairy Woodpecker of southern Michigan, particularly on the Edwin S. George Reserve. Extensive reference is made to literature pertaining to these two species and occasionally to other species of woodpeckers. Because of the presence of several similar species of Dendrocopos in Europe, frequent reference is made to the literature dealing with the European species.

It was found most satisfactory to discuss the Downy and Hairy together topic by topic and where adequate data were available to conclude each topic with a comparison of the two species and with the related European species. For example, under the topic "Feeding the Young" the Downy is discussed first, then the Hairy and this is followed by a comparison of the two species with reference to the European species.

The study of the Downy and Hairy has been divided into three Parts. Part 1 includes the nomenclature, distribution and description. Part 2 deals with the life cycle. In Part 3 such subjects as food, economic importance, migration, mortality factors, etc. are discussed. The numerous topics of each Part are listed in the Table of Contents.

Description

The subjects of study in this work are two species of vertebrate animals belonging to the Class Aves. They are placed in the Order Piciformes which may be distinguished by the following characters. Basiterygoid process absent; 14 cervical vertebrae; sternum four-notched; feet zygodactyl; nares impervious, holorhinal; tracheo-bronchial syrinx; 10 primaries; 10 to 12 rectrices. Young are hatched blind and naked, no down in young or adults.

The Family Picidae to which the two species studied belong, may be described as: Small to medium sized birds, bill usually powerful, more or less elongated and chisel-shaped. The claws, feet and legs are strong and adapted for climbing about in trees. The tail feathers are generally stiffened and used as a further aid in climbing about in trees. Twelve rectrices are usually present although the outer pair may be very short. Only 9 functional primaries, the tenth being very short. The salivary glands are highly developed. The hyoidean apparatus is peculiar, there is no urohyal bone, the ceratohyals are small and fused together; the basihyal is slender, generally the thyrohyals are enormously developed and curl up over the skull. The apparatus is actuated by correspondingly developed specialized hyoidean muscles which thrust the long lubriciform tongue far out of the mouth. The Picidae are absent from Madagascar, Australia and Polynesia. They are wood-land birds and generally solitary in their habits. Their food is largely larvae and the eggs of tree inhabiting insects although

several forms descend to the ground to secure ants. All deposit their eggs in hollows in trees and most species excavate their own nest cavities. Without exception the eggs are white.

Ridgway (1914:194-195) described the genus Dendrocopos and based his description on all of the American species and D. major, D. minor, D leucotus and D. medius only of the Old World forms. His description is quoted here "Rather large to very small Picinae (wing 90-150mm.) with outer hind toe decidedly longer than outer front toe, longest primaries exceeding secondaries by more than one-fourth (but less than one-third) the length of wing, outermost (tenth) primary about one-third as long as ninth, culmen longer (usually much longer) than outer hind toe with claw (or else with tuft of antrorse prefrontal plumes covering basal half of maxilla); outer webs of primaries (at least) spotted with white, lateral rectrices white (with or without black bars or spots), upper parts black or (rarely) brown, often barred or striped with white on back, under parts whitish, with or without darker markings.

"Bill usually shorter (sometimes very much shorter) than head, rarely slightly longer, distinctly chisel-shaped at tip, its width at anterior end of nostrils about equal to its depth at same point; culmen straight or very faintly convex, sharply ridged; gonys twice as long as mandibular rami, or slightly more, more or less distinctly ridged, straight or very nearly so; supranasal ridge and prenasal groove very distinct, parallel with culmen, running out to (or toward) edge of maxilla at a point less than one-third to a little more than

one-third the distance from tip to base of tomium. Nostril small, longitudinally elliptical or linear (sometimes more pointed anteriorly), situated nearer to tomium than to culmen, completely covered by a conspicuous antrorse tuft of hair-like, bristly-tipped prefrontal feathers. Feathers of malar apex and chin antrorse, bristle-tipped, the latter covering base of gonys. Orbital region partly naked, the margin of lower eyelid and posterior portion of upper eyelid clothed with minute feathers. Wing rather long, the longest primaries exceeding secondaries by more than one-fourth (but less than one-third) the length of wing; sixth and seventh, sixth, seventh and eighth, or seventh and eighth primaries longest, and the ninth much shorter than fifth (sometimes a little shorter than fourth), the tenth (outermost) about one-third as long as ninth. Tail nearly two-thirds as long as wing, the rectrices broad, the middle ones more or less strongly decurved terminally and with tip gradually short-acuminate. Tarsus longer than outer hind toe with claw (except in D. scalaris, D. nuttallii, D. stricklandi, and D. arizonae), feathered in front for at least upper third; outer hind toe much longer than outer front toe."

The Hairy Woodpecker, Dendrocopos villosus villosus, has been described in detail by Ridgway (1914:201-204). "Adult male. --Pileum uniform glossy blue-black; a nuchal band of bright poppy red or scarlet, usually interruped in middle portion by an extension of the black of pileum; rest of upper parts black, the median portion of back (broadly) white, the wings (including middle coverts) spotted with white, the spots on greater coverts and remiges arranged in

regular transverse series; two lateral rectrices, on each side (including outermost rudimentary rectrix), entirely white, the third white except basal portion of inner web, the fourth with greater part of outer web and distal portion of inner web white; nasal tufts dull white to dull brownish yellow, the bristly shafts blackish; a broad white supra-auricular stripe, narrower anteriorly, where extending over eye (sometimes confluent with whitish of nasal tufts); a broad white suborbital-subauricular stripe, anteriorly confluent with whitish or dull yellowish of nasal tufts, posteriorly extending to sides of neck; between these two white stripes a broad black stripe involving whole of auricular region and part of suborbital region, posteriorly confluent with black of hindneck; a black malar stripe (usually more or less broken anteriorly by admixture of white), continued and gradually widening, posteriorly, where confluent with a lateral extension of the black of hindneck, and also sending off a short branch along side of chest; underparts immaculate white; bill deep grayish horn color, the mandible slightly paler; iris reddish brown (claret brown to burnt umber); legs and feet dull grayish blue, bluish gray or grayish olive; length (skins), 184 - 228 (220); wing, 114.5-124 (120.4); tail, 65-77 (71.4); exposed culmen, 27-33 (29.2); tarsus, 21-23 (21.9); outer anterior toe, 13-15.5 (14.4).

"Adult female.--Similar to the adult male but without any red on head; length (skins), 185-231 (206); wing, 115-128 (119.9); tail, 68.5-83 (74.2); exposed culmen, 25-30 (27.3); tarsus, 20-23 (21.1); outer anterior toe, 13-15 (14).

"Young male.--Similar to the adult male, but without any red nuchal patch, the crown, however, streaked or spotted with red (usually more or less pale--sometimes pale yellowish or pinkish), the reddish or yellowish tips to the feathers often preceeded by a small spot or streak of white; black parts of plumage duller.

"Young female.--Similar to the young male, but without any reddish or yellowish on crown, which, however, is sometimes minutely streaked or spotted with whitish."

Ridgway's (1914:228-230) description of the Downy Woodpecker, Dendrocopos pubescens pubescens is quoted here. "Adult male.--Pileum, auricular region, median portion of hindneck, sides of interscapular region, scapulars, and upper tail-coverts, black, faintly glossed with bluish; four middle rectrices black, without gloss; wings dull black, passing into dark brownish slaty on primary coverts and terminal portion of primaries, the middle coverts with a rather large mesio-terminal roundish, guttate, or cuneate spot of white and a sub-basal roundish or transverse spot of the same; greater coverts with a roundish sub-terminal spot of white on outer web and a sub-basal roundish spot (concealed) of same on both webs; secondaries crossed by four transverse series of roundish white spots, the first concealed by greater coverts, the last smaller and terminal; outer webs of primaries with similar but more elongate and quadrate spots, about four in number on longest quills besides a smaller terminal spot or margin; a broad median stripe of white on back, this sometimes slightly streaked or flecked with black; two lateral rectrices, on each side, white or dull white, with two

broad black bars across distal portion, the proximal one usually broken or interruped; third rectrix with distal half, more or less, of outer web white, the terminal portion of inner web with one or more broad white bars or spots; nasal tufts dull white, the bristle-like shafts black terminally, a white supra-auricular stripe, continued, narrowly, above eye, its posterior end in contact with a bright red nuchal band; a broad subauricular stripe of white, extending anteriorly, beneath eye, to lores, where confluent with the duller white of nasal tufts, its posterior end involving sides of neck, including post-auricular region, except upper portion; malar region grayish, intermixed with black, anteriorly (sometimes wholly black except extreme anterior portion), posteriorly continued as a gradually widening "solid" black stripe which curves upward behind the white cervical area and connects with the black of back; under parts plain pale brownish gray or dull grayish white, more whitish on chin and throat, the under tail-coverts usually barred or flecked with black; under wing-coverts mostly immaculate dull white, but with a black patch on carpo-metacarpal region, inner webs of remiges dull slaty with large semiquatrate spots of white, except on distal portion of longer primaries; bill dark horn grayish, paler on mandible; iris brown or reddish brown; legs and feet dusky (olive-grayish in life);...

"Adult female.--Similar to adult male, but without any red on head, the red nuchal band replaced by a white one, this usually divided by a median black area; ...

"Young male.--Similar to the adult male, but without the red nuchal band, the occiput and more or less of crown, however, with feathers tipped with red (usually more or less pale), the crown often dotted with white; black areas duller (without gloss); under parts sometimes more or less streaked on chest and flanks.

"Young female.--Similar to the young male, but without any red on head."

The subspecies of Downy Woodpecker that I studied is Dendrocopos pubescens medianus and differs from the above description as follows: (Ridgway, 1914:233): "Similar to D. p. pubescens, but larger, and the whitish of under parts, etc., slightly paler (more nearly white)."

Ridgway (1914:233) gave the following measurements for D. p. medianus.

"Adult male.--Length (skins), 145-161 (153); wing, 91-96.5 (94.1); tail, 51-60.5 (55.8); exposed culmen, 15-17.5 (16.4); tarsus, 15-16.5 (16); outer anterior toe, 10-11 (10.5).

"Adult female.--Length (skins), 145-161 (153); wing, 91.5-97 (94.7); tail, 50-61.5 (56.4); exposed culmen, 14.5-17.5 (15.4); tarsus, 15-16.5 (15.4); outer anterior toe, 9.5-11 (10.4)."

The descriptions of the Downy and Hairy are very similar, the only difference in addition to size is the markings on the outer retrices. Voous (1947:74) has commented on the close similarity of these two species. "...Taxonomically pubescens may be characterized as the minor edition of villosus, both species especially have in common the broad black eye stripe, the white median dorsal stripe, and the

uniform (unstriped) underside, even in juvenile plumage. Apart from the relatively smaller and feeble bill of pubescens differences exist in the color pattern of the lateral rectrices only:

"villosus: lateral pair of rectrices uniform white; outermost but one with a broad uniform white tip, but usually with a black patch at the base of the inner web.

"pubescens: Lateral rectrices broadly barred with black and white.

These differences, however, do not appear to be principal ones, since in one of the Bahaman races of villosus (piger)'one or more black spots on inner webs of two lateral pairs of normal rectrices' are stated to occur regularly (Ridgway, 1914, p. 209), and an additional island race (picoideus: Queen Charlotte Islands, British Columbia) has been characterized by having 'the lateral rectrices sometimes spotted or broadly barred with black' (Ridgway, 1914, p. 220), besides, a few cross bars have been found by me on two outermost pairs of tail-feathers in a ♀ from Costa Rica (extimus: Leiden Mus.). In northern specimens of pubescens the black bars are much reduced in size, becoming nearly obsolete in some specimens of the race nelsoni (Ridgway, 1914). The proportional differences between villosus and pubescens, which are conspicuous in northern and temporate birds, become less defined when the southern races of both species are compared (average measurements of ♂: Ridgway, 1914):

"v. extimus (mountain zone Costa Rica): wing 102.8; culmen 24.9; tail 58.6 mm.

"p. gairdneri (costal humid zone of California): wing 95.1; culmen 16.4; tail 58.1 mm.

"Relative small measurements of culmen, tarsus, and middle toe in a subspecies of villosus are also found in the race parvulus from north-central Salvador of which the following measurements are of interest (average of 3 adult males: Dickey and Van Rossem, 1929, p. 220):

"v. parvulus (mountain zone of Salvador): wing 103.3; culmen 21.4; tail 59.3 mm."

Nomenclature

No special attention has been paid to the nomenclature of the birds studied here. I have followed the terminology used by Peters (1948) for the family Picidae. The generic name of the Downy and Hairy Woodpeckers has recently been changed. The name **Dendrocopos** was first proposed for this genus by Koch in July, 1816 but was later declared a synonym of Dendrocopus, a name proposed for another genus of birds by Vieillot in April, 1816. The International Rules of Zoological Nomenclature state that generic names which differ only in the ending or form are valid when properly published. Dendrocopos Koch has therefore been revived as the proper name of this genus and replaces Dryobates Boie.

Distribution

The family Picidae is almost world-wide in its distribution, it is absent only from Australia, Polynesia and Madagascar. The genus Dendrocopos is nearly as widely distributed as the family, being absent in addition to the above regions also from southern Africa and the northern half of South America. The ranges of the species Dendrocopos villosus, the Hairy Woodpecker, and D. pubescens, the Downy Woodpecker, are shown on Map 3. Also shown are the ranges of the subspecies I studied in the field, Dendrocopos villosus villosus and D. pubescens medianus. The range of Dendrocopos pubescens is entirely within that of D. villosus and the ranges of the subspecies mentioned above are nearly the same.

Explanation of Map 3

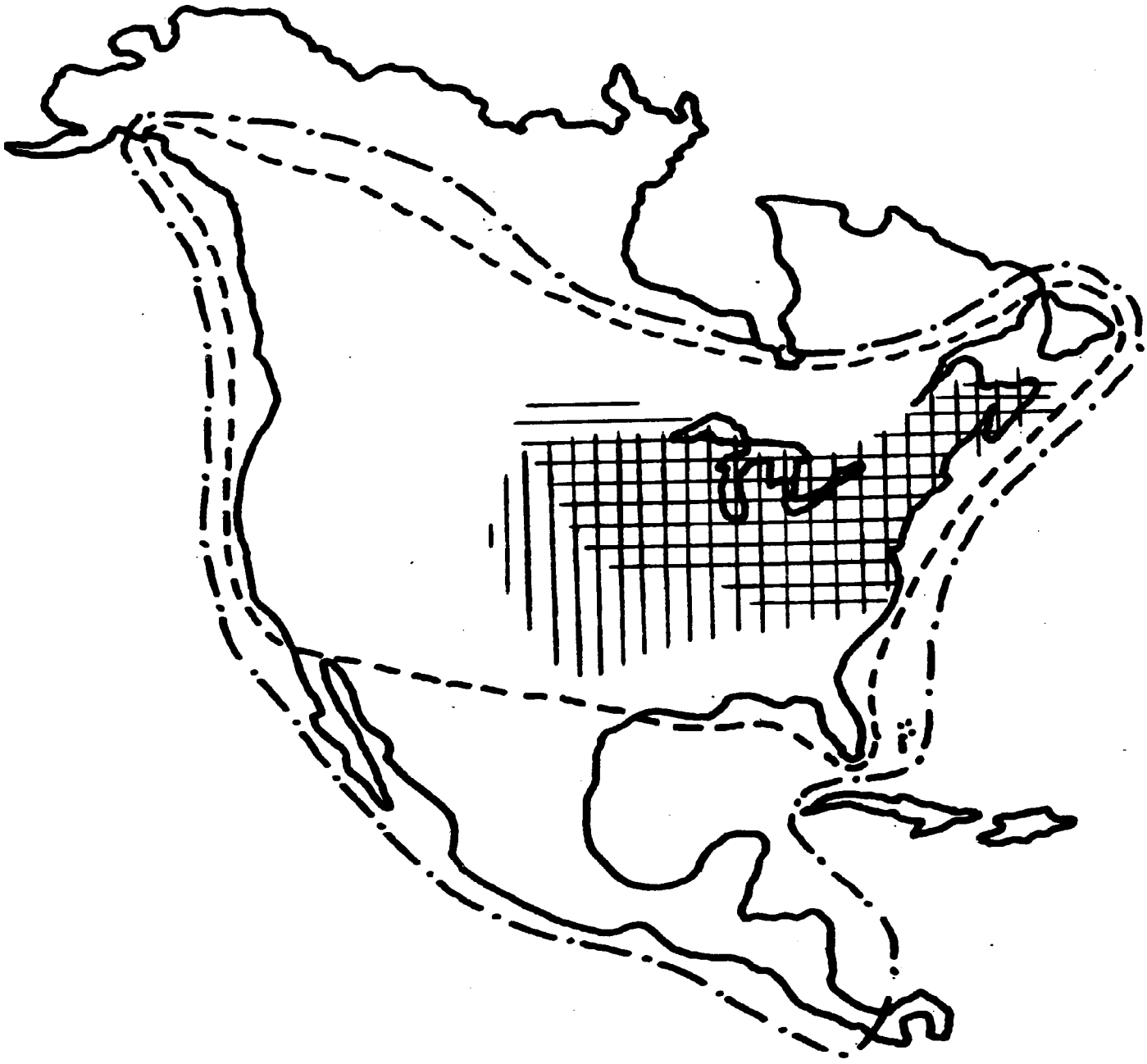
Distribution of the Species *Dendrocopos villosus* and *D. pubescens* and the Subspecies *D. v. villosus* and *D. p. medianus* in North America.

The range of *D. villosus* is indicated by the dash-dot-dash line.

The range of *D. pubescens* is indicated by the broken line.

The range of *D. v. villosus* is indicated by the vertical lined area.

The range of *D. p. medianus* is indicated by the horizontal lined area.



MAP 3

Wintering Area

Downy

According to the literature, the Downy tends to avoid others of its kind during the winter. Forbush (1927:262) has said "... during the winter Downy seems rather to shun its own kind,... Quite commonly, however, one may be seen with some band of Chickadees and Nuthatches,..." Stone (1937:668) made a similar statement, "While not associating with its own kind to any extent the Downy is often found in one of the winter assemblages of chickadees, nuthatches, kinglets etc.,..."

Tyler (Bent, 1939:66) stated "The downy is not a bird that ranges widely in search of food; moreover, for protection against the weather it is held to the vicinity of its roosting hole. Therefore each bird, in order to be sure of sufficient food for itself during the cold months, must maintain dominion over a territory large enough to support it through the winter.

"...The families disperse, and until the next breeding season each individual becomes a solitary bird, living in a restricted region, while it defends against trespass, resenting and repelling the approach of any other downy woodpecker."

The areas where certain marked male and female Downys wintered on the George Reserve in the winter of 1946-1947 are shown on Maps 4 and 5. Male Downys I, P and T and female Downys H, I, J, K, T, U, and V remained for the most part in the vicinity of the trap where each had been captured, these traps apparently being in or very near the wintering area chosen by these individuals. Males J and N and

females G and Q were frequently seen feeding at Trap 6 about 550 yards from their usual wintering areas. These individuals were sometimes found in the trees along the road east of my home, apparently travelling between their respective areas and Trap 6. Male S and female M visited Traps 6 and 7 with equal frequency. The Southwest Woods and the Southwest Swamp were the wintering area of males K, U and V and female N. Male V visited Trap 8 for food whereas the other three individuals visited Trap 7 for food.

As far as I was able to determine, during the winter the Downys had no special area or territory they claimed as their own, that is to say, defended against other Downys. The border between the Southwest Woods and the Southwest Swamp was a favorite place for Downys during the winter. This was the general wintering area of males K, U and V and female N. Here I sometimes saw two, three, or four Downys all feeding quietly within a few hundred feet of each other. In addition to the four individuals mentioned, females O and R may have wintered there also.

Male V moved about more than the other individuals in that area. As mentioned before, he fed at Trap 8 instead of at Trap 7 as did the other individuals wintering there. The wintering ground of Male V seemed to be the northwestern quarter of the Southwest Woods. This area was exposed to the prevailing northwestern winter winds and his frequent occurrence in the southeastern quarter of the woods may have been induced by his seeking a more sheltered area on certain days. The effects of strong winds on local winter distribution of birds in woodlots has been pointed out by Johnston (1942).

I have not attempted to establish the exact size of the wintering area occupied by a Downy on the George Reserve in the winter of 1946-1947. If one were to include the entire range over which any one individual Downy was known to have occurred during the winter, that wintering area would be 100 acres or more in size. However, if one included only that area where the individual was found more regularly and disregarded the foraging trips for food outside of that range, then the wintering area would be only 10 to 20 acres in size. The areas indicated on the maps for the individual male and female Downys represent where each individual was most regularly found exclusive of its wanderings to and from the traps.

In summary, the evidence indicates that the Downys on the George Reserve do not establish winter territories which they defend against trespass by other Downys. Frequently two or more Downys wintered in the same area and in complete harmony with each other.

Hairy

Apparently the Hairys on the Reserve occupied large areas during the winter. During the winter of 1946-1947, two Hairys (male A and female B) were found anywhere from the Northwest Woods south to the trap at the Headquarters House. This area was about 800 acres in size of which approximately 250 acres were wooded. I did not observe any defense of a wintering area by a Hairy.

Another pair of Hairys maintained a wintering area in the Southeastern corner of the Reserve and adjacent woodlots. Both of these

Explanation of Map 4

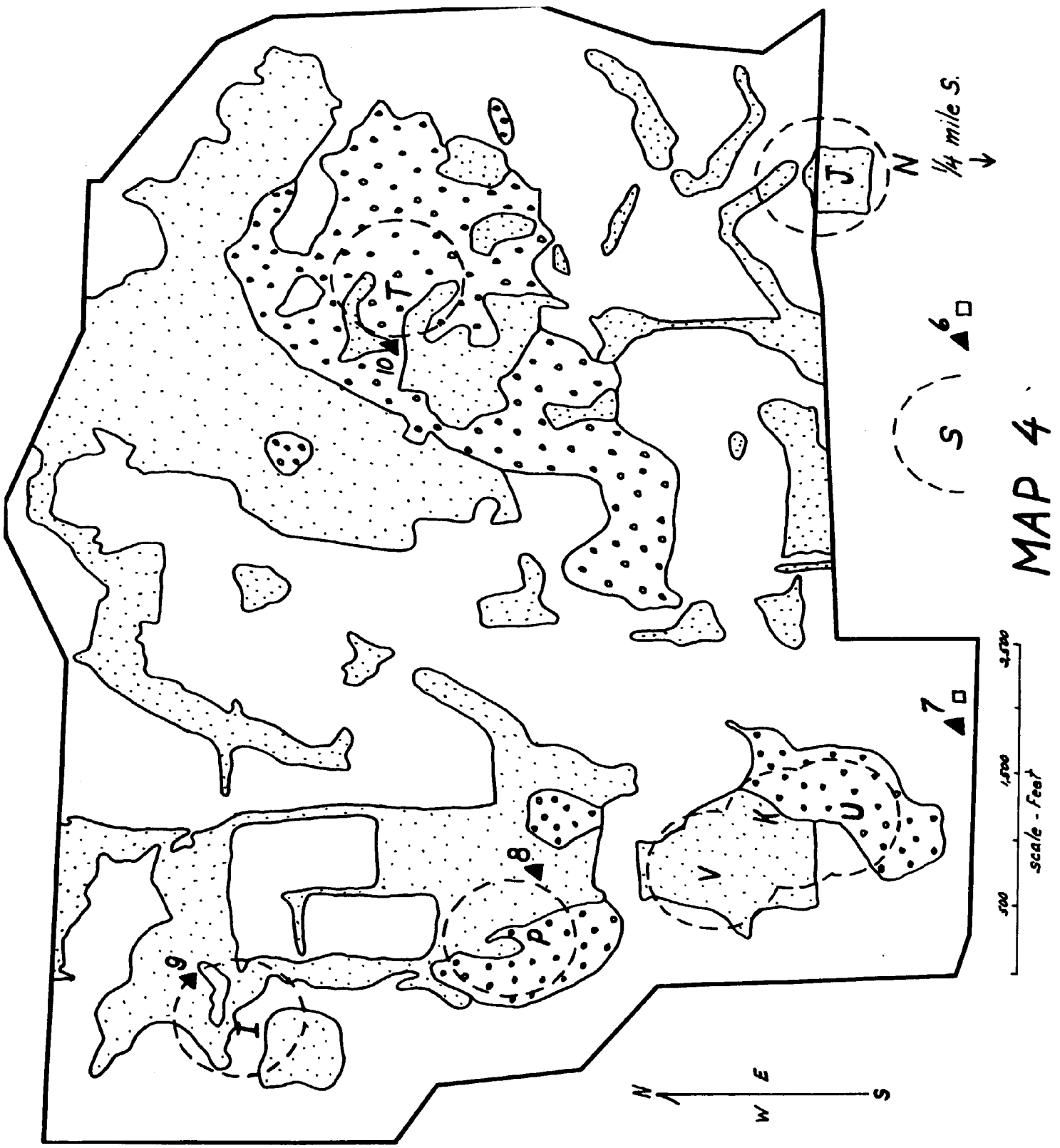
Wintering Areas of Male Downy Woodpeckers on the George Reserve During the Winter of 1946-1947

The letters indicate the identity of each male.

The broken lines are not intended to mark the limits of a territory; they indicate the area where each male was most frequently found.

The traps in operation during this period are indicated by solid triangles.

Oak-hickory woods are indicated by stippling and the forested swamplands, largely tamarack, are shown by open dots.



MAP 4

Explanation of Map 5

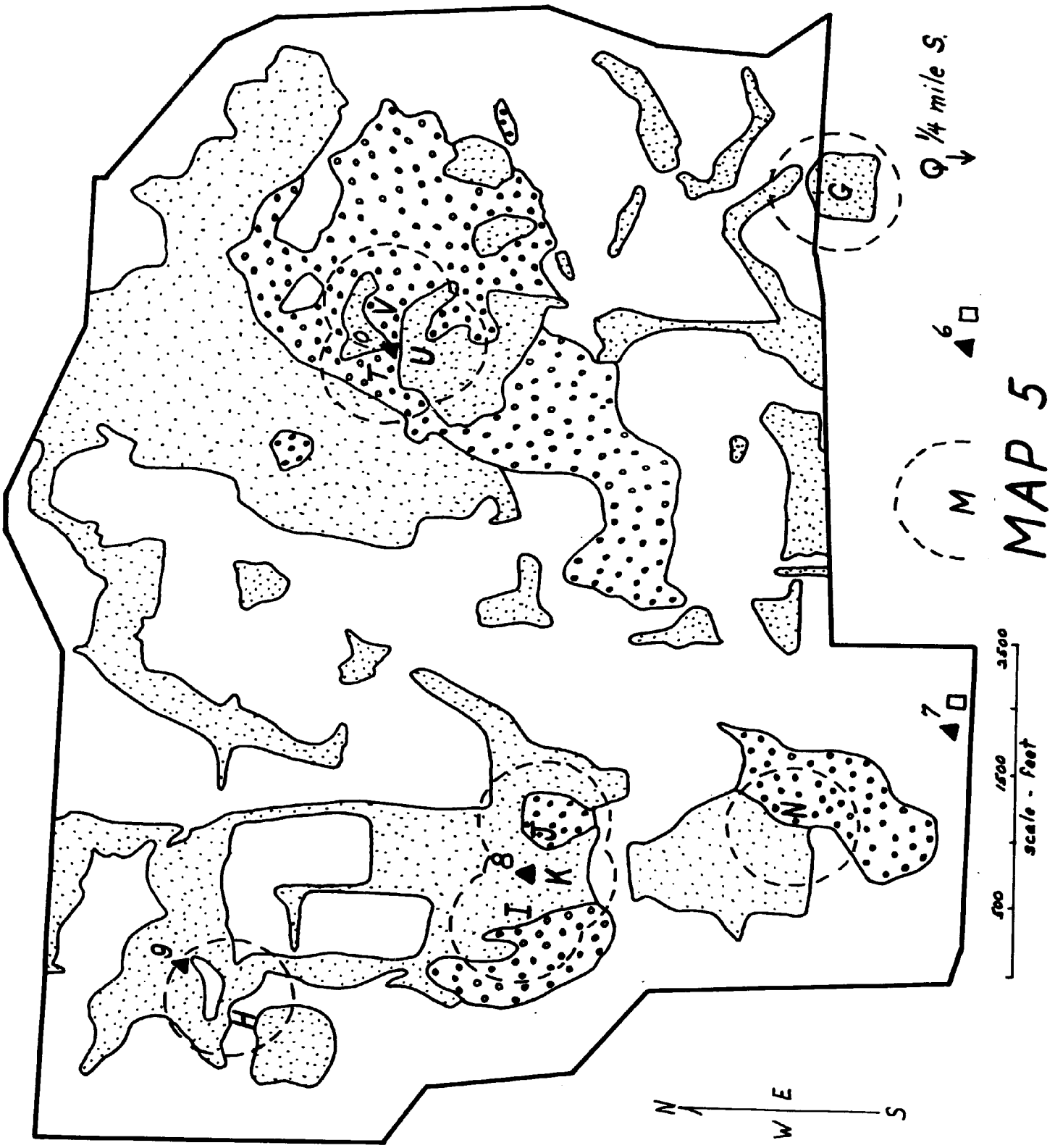
Wintering Areas of Female Downy Woodpeckers on the George Reserve During the Winter of 1946-1947.

The letters indicate the identity of each female.

The broken lines are not intended to mark the limits of a territory; they indicate the area where each female was most frequently found.

The traps in operation during this period are indicated by solid triangles.

Oak-hickory woods are indicated by stippling and the forested swamplands, largely tamarack, are shown by open dots.



MAP 5

birds were frequent visitors in the trees about my home but never visited the trap there. A third pair wintered in the extensive wooded area of the northeastern quarter of the Reserve. Very few data were secured for this pair, the male (B) of which was caught at Trap 10 on March 10, 1947. The wintering areas of the Hairys on the Reserve during the winter of 1946-1947 are shown on Map 6.

Explanation of Map 6

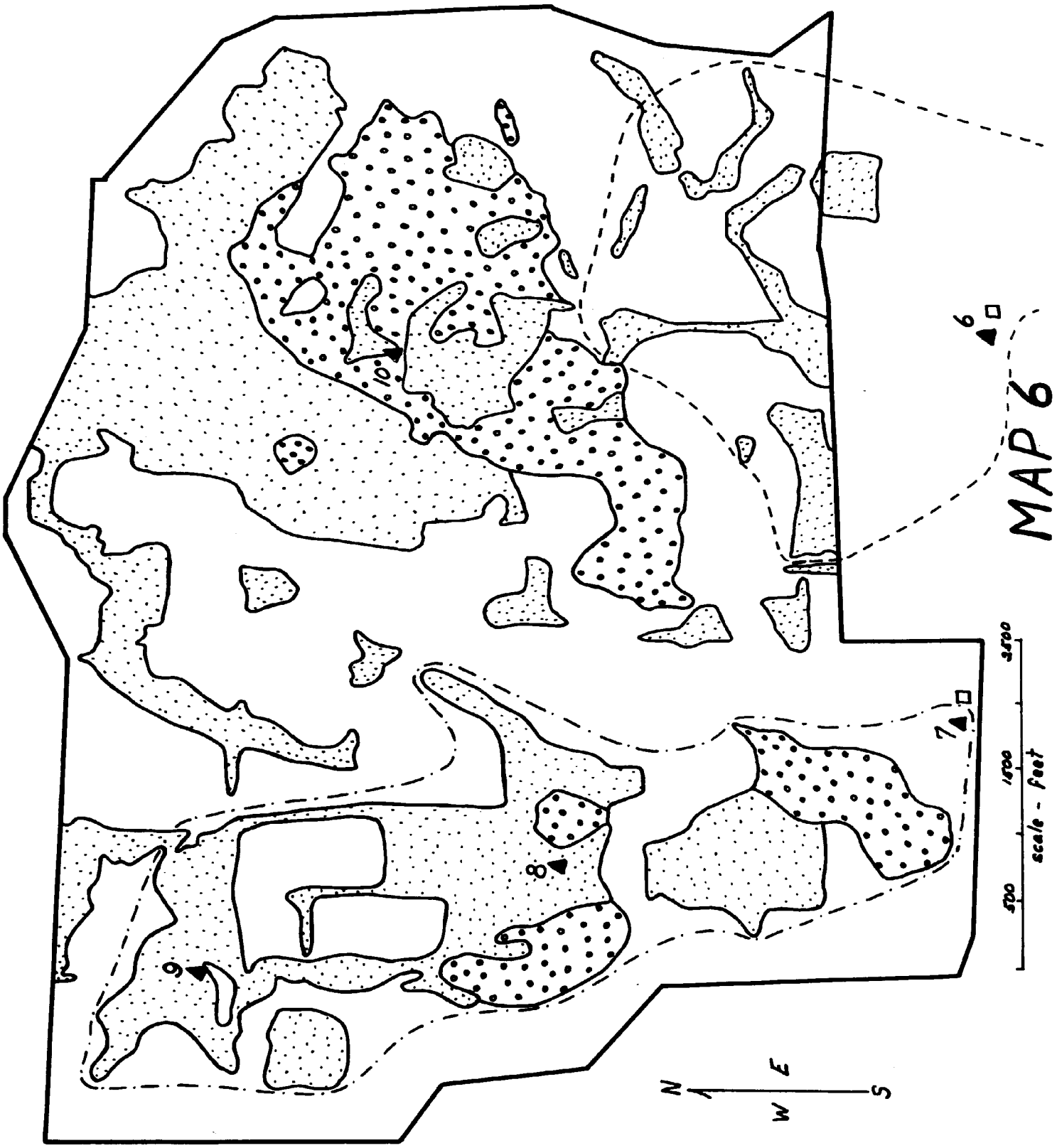
Wintering Areas of Hairy Woodpeckers on the George Reserve During the Winter of 1946-1947.

The wintering area of Pair 3 (male A, female B) is outlined with a dash-dot-dash line.

The wintering area of Pair 4 (neither bird marked) is outlined with a broken line.

Traps in operation during this period are indicated by solid triangles.

The oak-hickory woods are shown by stippling, the forested swampland, largely tamarack, by open dots.


MAP 6
6
7
8
9
10
N
E
S
W
500
1000
2000
scale - feet

Association Between Sexes During the Winter

I observed no action by the Downys during the winter that indicated sex recognition and no evidence that they wintered together as mated pairs.

It was quite different with the Hairys. I followed one pair of color-banded Hairys from December 1946 through the nesting season the following summer (male A and female B). Throughout the winter these two birds were always found fairly close to each other and there was no evidence at all that they maintained separate territories during the winter. Shelley (1933:204-205) stated that the male and female Hairys kept separate, although adjacent, winter territories.

Association Between the Downy and Hairy and other Species of Birds During the Winter

The association between Downys and Hairys during the winter was purely passive. The Hairys, being less trusting and more wary than the Downys, generally came to the traps only after they had watched one or more Downys feed there. The Downys always left the traps whenever a Hairy came to feed and I did not see a Downy ever offer any show of resistance against a Hairy. Twice I watched two Hairys feed at the same time on a piece of suet at a trap (Jan. 27 and Feb. 6, 1947). They were a mated pair (male A, female B). Quite frequently two and sometimes three Downys fed at the suet together.

Usually neither a Downy or Hairy objected if a Chickadee, Titmouse, or White-breasted Nuthatch fed at the suet with them. The woodpeckers would feed on one side of the suet and the other birds on the opposite side. A few Downys were very aggressive and would not tolerate the presence of others of their kind or any other small bird.

I frequently found one or more Downys feeding in company with a mixed flock of Chickadees, Titmice, and Nuthatches. The Downys fed and mingled with the other birds as the flock progressed slowly through the woods. However, the Downys generally remained behind whenever the flock moved away from their winter home range. Occasionally a Hairy was present in the flock, but only by accident. The Hairy either suddenly departed or remained while the flock moved on.

Pair Formation and Courtship

Before describing the pair formation and courtship activities of the Downy and Hairy Woodpeckers as I believe they occur, it is perhaps advisable to give my definitions of terms. In Webster's Dictionary, pair formation is defined as: the action by which a male and female create a couple. As it is the pair formation related to the breeding cycle which is of primary importance, pair formation may be more accurately defined as: the action by which a male and female create a couple for breeding purposes.

The creation of a couple or pair does not mean that breeding immediately follows. Each individual of a pair must attain a certain physiological and psychological state or level before copulation, nest building, and egg laying can occur. Such actions that are believed to lead to that level are here called courtship activities. Courtship in birds may thus be defined as the reaching of physiological and psychological levels necessary for reporduction.

Defined in this manner, pair formation and courtship are separable. Thus, in a monogamous species of bird, the male must first induce the female to remain on his territory and accept him as her mate. Following the successful completion of this action, the two individuals of the pair follow through a series of actions - courtship activities - the goal of which is the laying of fertile eggs. Such is the type of breeding behavior pattern that I believe the Downy and Hairy Woodpeckers follow. My data are admittedly inadequate. It was only during the last season of study that I interpreted the breeding behavior of the woodpeckers in this manner.

Pair Formation

Downy

In the winter of 1946-1947 I observed a definite movement by the female Downys on the Reserve from their respective wintering area to another area in which they eventually nested. This shifting occurred in the last half of February and early March. The movements are shown on Map 7 and certain other data are summarized on Table 4.

Females T and U both appeared at Trap 6 at my home on March 30. This was a distance of 1,400 yards south of their wintering area. Female T was not seen again but female U continued to feed at the trap almost daily until mid-June. She nested (Nest 18) in the West Tamarack Swamp, more than a mile from Trap 6 and almost a mile from her wintering area.

Female M visited Traps 6 and 7 regularly until late February, after which she was seen only at Trap 7. She nested (Nest 16) in the Southwest Swamp, 1,050 yards from her wintering area. Female K was a regular visitor at Trap 8 until early March. On March 21 she was seen at Trap 7 but was not seen again. Female G apparently nested in a woodlot about one-half mile south of her wintering area, the time of her movement was not observed. Female N was a regular visitor at Trap 7 until early March. On March 14 she appeared at Trap 6 and was believed to have nested in a woodlot northeast of Trap 6, a distance of one mile from her wintering area.

Female I moved from the West Woods into the nearby Southwest Woods, a distance of about 400 yards. Female H was not found again

Explanation of Map 7

Early Spring Movement of the Female Downy Woodpeckers from Their Wintering Areas to Their Nesting Territories on the George Reserve in 1947.

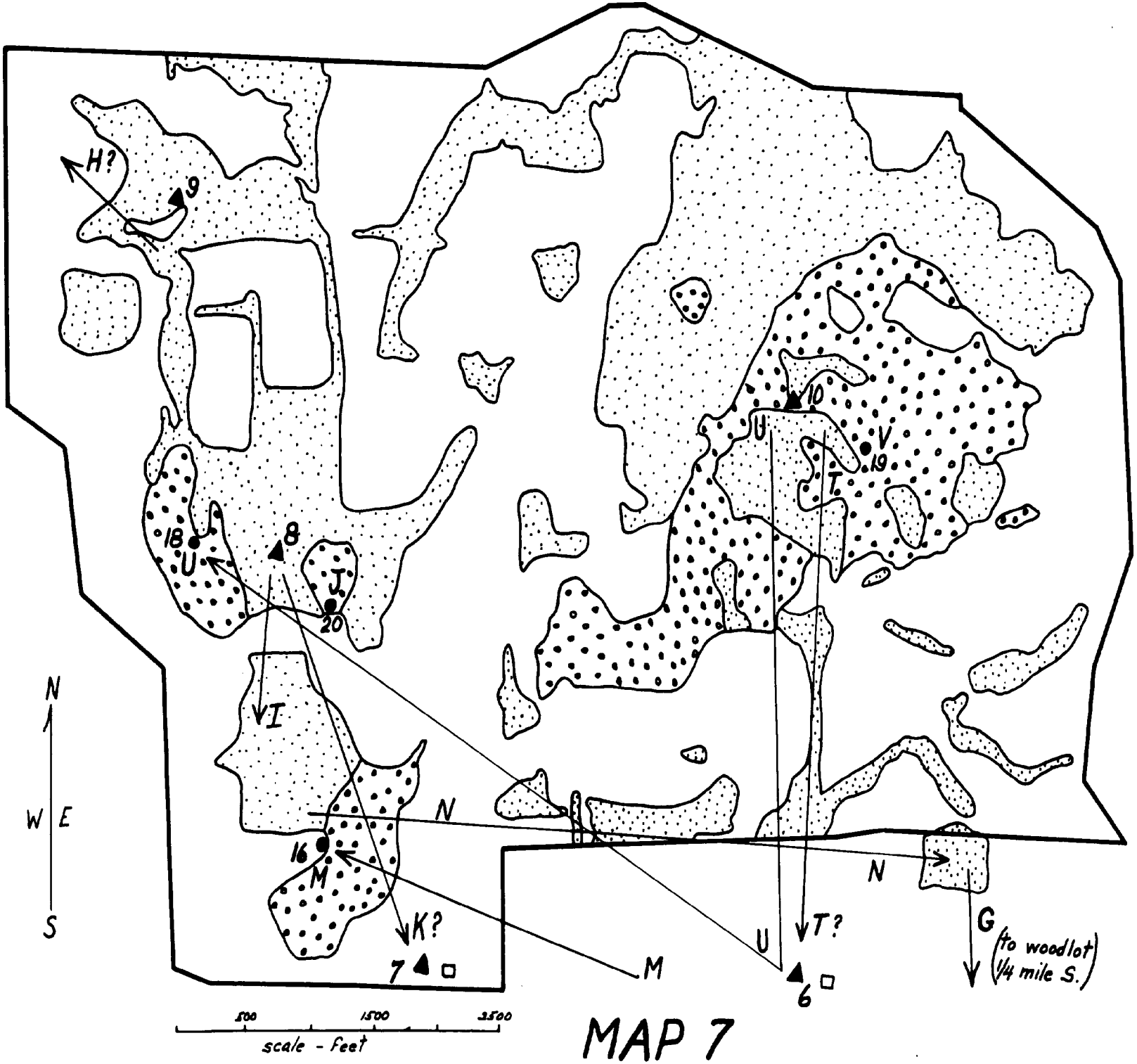
The identity of the females is indicated by letters.

Traps in operation during this period are marked with triangles.

Nests are shown with large solid dots.

The arrows extend from the wintering area of each female and end at the last known place that the female was seen. An arrow ending at a nest indicates that the female nested there; an arrow ending in some woodlot but without a nest indicates that the nest was not found although the female is believed to have nested in that area; a question mark at the end of the arrow indicates that the female was not found again after she had moved to that place.

Oak-hickory woods are stippled, the forested swamplands are marked by open dots.


H?
9
10
U
V
19
T
18
U
8
J
20
I
N
W
E
S
N
16
M
K?
7
M
U
T?
6
N
G
(to woodlot
1/4 mile S.)
500
1500
2500
scale - feet

MAP 7

Table 4

Summarization of Data Pertaining to the Early Spring Movement of the Female Downys on the Reserve in 1947.

Identity of female	Identity of males with which the females in column 1 wintered	Distance between the winter territory and the nesting territory of the females in column 1	Identity of the male with which each female in column 1 nested.	Nest No.
G	J	800 yards	N	
H	I	unknown	?	
I	P	400 yards	V	
J	P	none	unmarked	20
K	P	1100 yards	?	
M	S	1150 yards	K	16
N	K, U, V	1760 yards	J	
Q	N	1300 yards	?	
T	T	1650 yards	?	
U	T	none	?	18
V	T		T	19

after early February, and it is presumed either that she fell prey to some predator or moved to some other area. Two of the females did not move from their wintering area. These were females J and V. J mated with an unmarked male (Nest 20), and V mated with male T (Nest 19) whose wintering area was about the same as hers.

The mates of some of the females were not known. In these instances the females were not found again after they had left their wintering areas. Either they were subsequently overlooked or they had moved into a territory outside the study area. Eleven females were found to have moved an average of 940 yards from their wintering areas to their nesting territories. (See Table 4.)

I believe that the male and female of each pair of Downys separate sometime before winter and each bird establishes its own wintering area. The first step towards pair formation is the late winter movement by the females from their wintering areas. I do not know whether former mates reunite the following season as I was unable to devote another winter and breeding season to the problem. However, I suspect that pairs generally do remate each season.

Females J and V did not move from their wintering areas; they mated with males that had wintered in the same areas. It is possible that these two cases represent previously established pairs. Even those females that moved considerable distances may have been returning to their old mates. The movements of females G, I, M, and N appear to have been deliberate (see Map 7). In each case these females were each found in only two places --

their wintering areas, then their nesting territories. Had any of these four birds wandered about much I would have found them in more places. The fact that female U was found in more than two places may indicate that she did wander about seeking a mate.

Not one of the male Downys was observed to have moved away from its wintering area. In every case in which the nesting territory of a color-banded male was determined in 1947 on the Reserve, that area was the same as the wintering area of that male. Where two or more males appeared to have occupied the same wintering area, their respective nesting territories were adjacent and all within the general region they had jointly occupied during the winter. The close association of males K, U, and V during the winter was pointed out in the discussion of Wintering Areas.

Hairy

Very little was discovered about pair formation in the Hairy Woodpecker. Birds once mated apparently remain mated for the rest of their lives. Male A and female B were almost always found in the vicinity of each other throughout the winter of 1946-1947. Their nest was found in 1947 (Nest 3) and also in 1948 (Nest 6). I believe that these birds were paired when I first found them in December, 1946. Some courtship activities between male A and female B were observed in the spring of 1947 during the time of egg-laying and incubation. However, I did not see any activities by them which I felt were related to pair formation.

It is possible that pair formation in the Hairy occurs early

in the spring, probably during late February and March on the Reserve. These activities would be limited to young birds seeking their first mates or old birds whose mates of the previous year had been lost or old birds that for some other reason were unmated. Male C and female C were first seen to visit Traps 7 and 6 respectively two or three days before their capture. No unbanded males had been seen at Trap 7 or unbanded females at Trap 6 prior to the taking of male C or female C at their traps of capture. Male B, although not captured and color-banded until mid-March, was nevertheless frequently seen in the vicinity of Trap 10 all winter.

It is probable that male C and female C began wandering from their respective winter territories sometime in February, presumably to seek a mate. Male C apparently found a mate for he was seen several times at Trap 7 with an unbanded female that had been visiting Trap 7 irregularly that winter and early spring. Evidence indicated female C did not find a mate.

Comparison

From what few data I secured on the pair formation of Dendrocopos pubescens and D. villosus, it is apparent that a marked difference exists between the two species. On the George Reserve the pairs of D. villosus did not break up after completion of the breeding season but rather the male and female of each pair remained together. This was not found to be true with D. pubescens; in this species the pairs broke up after completion of the breeding season and wintered as individuals, not as mated pairs.

I have been unable to find much information about the mating for life of the European species of Dendrocopos. Steinfatt (1937:47) believed that the male and female D. major remained in the same territory after the nesting season but other workers do not verify his findings. Pynnonen (1939:80) stated that with D. minor the male and female may remain in the breeding territory and may occupy the same winter feeding territory and occasionally even use the same roosting hole, but not together. D. minor may prove to be very similar to D. villosus. In Dryocopus martius the female remains in the nesting territory and the male wanders away to some other territory after the breeding season (Pynnonen, 1939:78). It would be interesting to know if the male D. martius moves from a winter territory to a nesting territory in a manner similar to that observed by me in the female Dendrocopos pubescens.

The drumming of the male Downy at Nest 4 is typical of the drumming pattern followed by many of the males. He drummed for five or ten minute periods several times a day during April and early May. By the middle of May he was drumming almost constantly; on May 17 he drummed 157 times in one hour and on May 20, 290 times in 45 minutes. On May 24 no drumming was heard, and later that day he was found with his mate, busily excavating a nest.

In 1947 the drumming by the Downys gradually increased in amount throughout February and early March. It was during this period that the females left their wintering areas. However, instead of a continued increase in the amount of drumming as had been observed in 1940 and 1941, the drumming stopped almost entirely. Only two or three Downys continued sporadic drumming as the 1947 season progressed. The months of April, May and June were abnormally cold with unusual amounts of snow, rain and cloudy weather. Perhaps the adverse weather of 1947 had an effect on the drumming of the Downys on the Reserve that year.

I assume that the movement of the females as observed in the late winter of 1947 also occurred in 1940 and 1941. The female Downys must have moved into their nesting territories three to six weeks before the period of greatest amount of drumming performed by the males. My field observations indicated to me that pair formation was completed by late March.

A male and female Downy were caught at Trap 1 on March 16, 1941, and each marked with a colored feather in the tail. These birds were always seen together thereafter and their nest was subsequently

I have been unable to find much information about the mating for life of the European species of Dendrocopos. Steinfatt (1937:47) believed that the male and female D. major remained in the same territory after the nesting season but other workers do not verify his findings. Pynnonen (1939:80) stated that with D. minor the male and female may remain in the breeding territory and may occupy the same winter feeding territory and occasionally even use the same roosting hole, but not together. D. minor may prove to be very similar to D. villosus. In Dryocopus martius the female remains in the nesting territory and the male wanders away to some other territory after the breeding season (Pynnonen, 1939:78). It would be interesting to know if the male D. martius moves from a winter territory to a nesting territory in a manner similar to that observed by me in the female Dendrocopos pubescens.

Courtship

Downy

Drumming was heard occasionally during the late fall and early winter (October through December). In January and February, especially on quiet sunny days, I heard it more frequently and by early March several Downys were heard drumming in one day (five on March 9, 1941).

During the winter months the Downys were quite wary and it was difficult to approach a drumming bird to determine its sex. It appeared that male and female Downys drummed with about equal frequency during January and February. Females drummed occasionally throughout the spring until nest construction started. The drumming of the males increased steadily during March and April and reached a peak three to five days before nest construction started. As the nesting season approached, drumming birds became less wary and it was comparatively easy to make sex and color-band identifications.

In 1940 and 1941 the drumming of the male Downys continued to increase throughout March and April. In 1941, the drumming reached its greatest intensity during the last week in April. By the first of May that year nest construction had started. In 1940 the greatest amount of drumming was heard during the second week of May and nest construction started by mid-May. In each year there was a sudden decrease, almost a complete cessation, in the amount of drumming when nest construction was begun.

The drumming of the male Downy at Nest 4 is typical of the drumming pattern followed by many of the males. He drummed for five or ten minute periods several times a day during April and early May. By the middle of May he was drumming almost constantly; on May 17 he drummed 157 times in one hour and on May 20, 290 times in 45 minutes. On May 24 no drumming was heard, and later that day he was found with his mate, busily excavating a nest.

In 1947 the drumming by the Downys gradually increased in amount throughout February and early March. It was during this period that the females left their wintering areas. However, instead of a continued increase in the amount of drumming as had been observed in 1940 and 1941, the drumming stopped almost entirely. Only two or three Downys continued sporadic drumming as the 1947 season progressed. The months of April, May and June were abnormally cold with unusual amounts of snow, rain and cloudy weather. Perhaps the adverse weather of 1947 had an effect on the drumming of the Downys on the Reserve that year.

I assume that the movement of the females as observed in the late winter of 1947 also occurred in 1940 and 1941. The female Downys must have moved into their nesting territories three to six weeks before the period of greatest amount of drumming performed by the males. My field observations indicated to me that pair formation was completed by late March.

A male and female Downy were caught at Trap 1 on March 16, 1941, and each marked with a colored feather in the tail. These birds were always seen together thereafter and their nest was subsequently

discovered. This pair was certainly formed at the time of their capture. The drumming pattern followed by this male was very similar to that previously described for the male at Nest 4. The actions of other pairs of Downys were similar to that of the pair above. Whenever I was able to accumulate sufficient data for a pair it was apparent that the vigorous drumming of the males was an action that followed completion of a pair formation.

To summarize the above discussion, it appears that the drumming employed by the Downys is of little importance in pair formation. In the few cases where I was able to secure adequate data they indicate that pair formation was completed before the period of intensive drumming by the male. Drumming is a courtship activity performed by both sexes but mostly by the male.

Both sexes of the Downy take an active part in other courtship activities of the species. The male is the aggressor during these actions and the response of the female varies from almost utter indifference to enthusiasm as great as that of the male.

Courtship activities usually start in mid-March. At first these actions are half-hearted but by April they are performed with considerable fervor. On March 10, 1940, I watched a male Downy chase a female among the branches of a large tree. Neither bird made any sound. After two minutes of pursuit the male stopped and the female flew into another tree. After feeding quietly for 10 minutes the male suddenly started chasing the female again. He stopped in less than two minutes and shortly thereafter flew out of sight. The male was not especially agressive when pursuing the

female, he simply flew to where she was perched, causing her to move to some other place.

I saw a more spirited action in the Ann Arbor area several weeks later (April 21, 1940). A male Downy was aggressively chasing a female. Several times a minute the male gave voice to a series of short rapid "peenk" calls. He spread his tail feathers, raised and lowered the feathers of his crest and advanced towards the female with short jerky movements. Both birds moved the head and body from side to side, the tip of the tail remaining stationary. The entire body was stretched out with the bill pointed on the same axis as the line of the body. A few times I heard a short, sharp "whick" note uttered as the birds bobbed from side to side. The female attempted to avoid the male by dodging around the tree trunk or branch. The male was always behind or below her and when he came within 6 or 8 inches of her she flew to some other perch. After 15 minutes of this action the birds suddenly departed, together, from the woods.

On April 24, 1940, again the Ann Arbor area, I found a pair of Downys, both drumming. The two birds were about 30 feet apart. They suddenly stopped and one chased the other, I could not follow the sexes, into another woodlot but returned to their original drumming places a minute later and resumed their drumming. After several minutes they ceased drumming and commenced to feed quietly.

Apparently some courtship display is performed in the fall. On October 2, 1946, I found one male Downy chasing another male. They were first noted about five feet above the ground on the trunk of a

medium sized oak. Both birds held their tails partially spread but had the other feathers flattened close to their bodies including those of the head. Their necks were outstretched and their bills pointed straight ahead. All this served to give the birds a very slender appearance. They kept their legs quite stiff and straight, thus holding their bodies away from the trunks of the trees. They moved about on the trunk, one bird 10 to 18 inches above the other. The wings were partially opened and closed very rapidly and the head bobbed from side to side. The upper bird moved downwards toward the lower bird in short jerky steps, then the lower bird, after retreating a short distance started upwards, the upper bird then retreating. Thus they moved up and down the tree trunk. On a few occasions they came very close to each other and considerable wing flapping ensued, then they flew to another tree trunk and resumed the action. Only twice was actual body contact made between the birds. Most of the time they kept within sight of each other although sometimes they were on opposite sides of the trunk. In shifting about on the trunk, they frequently exchanged positions, the upper bird becoming the lower and the lower the upper.

The birds finally separated after 40 minutes of this action, and commenced to feed within sight of each other although apparently paying no attention to one another. They were quiet during most of the action but now and then I could hear a low "whic-cup" sound. A female Downy was feeding in the immediate vicinity and seemed to pay no attention to the two males. A male Hairy and another Downy whose sex was not determined were also nearby but neither paid any

attention to the activity of the two males.

Tyler (Bent, 1939:66-67) observed a very similar action between two female Downys. He stated "October 15, 1935. Two birds are in a large, bare maple tree; one is noticeably larger than the other, but neither one has a red occipital patch. They keep near each other, one following the other by short, quick flights. They perch perfectly motionless for a moment a foot or two apart; then both together sway their heads, swinging them quickly down and up to one side, down and up to the other side. The swing is very rapid, like the wink of an eye. They flit their wings upward and outward, also with the speed of a wink, over and over--all this without a sound. They fly behind a branch sometimes but keep mostly in sight of each other, and, although neither attacks, each seems wary of attack and dodges away when approached. They sometimes alight on very slender branches, and once a bird goes to the ground where it stands with its head held high up. They move very actively and lightly, with never the slightest blundering, flitting silently and easily from branch to branch."

MacArthur (1942:309) noted a male and a female Downy engaged in a somewhat similar activity on October 20, 1940. His account is as follows: "Stationed on a limb, head to head, they appeared to be engaged in courtship activities. The male was displaying before the female and in doing so he kept his head raised at a considerable angle to the long axis of his body. All the while he would flip his wings sharply, while he kept his tail fanned out. At times there was a slight weaving motion of the head, but it was

not a conspicuous part of the display. The female, in the meantime, received the affections of the male in a somewhat passive manner, although she occasionally flipped her wings. No sound was made by either bird, and they would remain on the same branch for perhaps a minute, then they would fly to another tree, and there repeat the performance. The female always made the first move to another perch."

Hairy

The drumming activities of the Hairy are apparently a part of the courtship activities of the species and not a part of pair formation. The Hairys at Nest 4 illustrate this very well. Neither bird was banded but I feel certain that the same individuals were observed each time. On April 29, 1947, the first drumming by a Hairy was heard. The drumming was in the woodlot southeast of my home and I saw the male Hairy drumming there several days later. During the early part of May the male drummed there frequently and I spent considerable time searching for the nest in that woodlot. Several times the male was seen to fly from his drumming spot into a small woodlot on the south border of the Reserve. After May 10 no drumming by this bird was heard. I found Nest 4 in early June and noted the day on which the young left the nest (June 6). Nest 4 probably was excavated late in April, egg-laying and incubation occurred during the first half of May and the young hatched by May 15. The male apparently drummed from the time excavation of the nest was started until incubation was well advanced. His drumming spot was not near the nest but in another woodlot about 800 yards south.

This Hairy drummed after pair formation was completed, even if one assumes that pair formation is completed just a day or two before nest construction starts. During the spring of 1940, 1941, and 1942, I observed Hairys drumming and in every instance the time of drumming eventually proved to be between the start of excavation of the nest and the hatching of the young.

Several times drumming seemed to be closely associated with the act of copulation. This was observed on March 9, 1941. I heard drumming in the Southwest Woods and after two or three minutes saw a Hairy fly toward the drumming bird and copulate with it. As the birds were several humdred feet away from me I could not determine their sex but believe that it was the female that had been drumming. On April 26, 1940, I watched a female Hairy drum for nearly 25 minutes. She finally went deeper into the woods and no other Hairy was seen in the vicinity.

To summarize the above, it seems that drumming is not related in any way to pair formation in the Hairy Woodpecker. Drumming may be a courtship activity and sometimes is associated with copulation.

I observed courtship activities other than drumming by the Hairy Woodpeckers during March. On March 9, 1941, a female Hairy was found quietly feeding in some tamaracks. As she flew to another nearby tree a male Hairy appeared and alighted a few feet from her. The two birds gave several "whic-cup" sounds that reminded me of a similar call note of the Flicker (Colaptes auratus). The birds commenced to dodge from side to side on the branchless trunk of a dead tamarack. They held their necks outstretched with their bills

pointed skywards. Much bobbing and nodding occurred with each bird constantly moving about on the trunk in short jerky movements, first to one side then to the other and gradually working towards the top of the stub. Most of the time they kept about 18 inches apart but when they came closer they partially opened and closed their wings rapidly. After three or four minutes of this action the female flew into the swamp. The male remained on the stub for several minutes quietly feeding there then he flew off in the direction the female had taken. I watched a very similar action in the Ann Arbor area on March 29, 1940. After four minutes of spirited activity the two birds became quiet and commenced to feed within 15 feet of each other.

The two observations just described are the extent of my observations for this species on courtship activities other than drumming or copulation. Apparently the Hairy does not indulge in intensive or frequent courtship activities.

Comparison

The courtship activities other than drumming were very similar for Dendrocopos villosus and D. pubescens. These activities were more commonly observed in pubescens than in villosus even when one considers the greater numerical advantage of the former. The extent of my observations indicate that the male and female of both species are equally active in the courtship activities. The activities as I have described them for D. pubescens and villosus are very similar to those of D. major and minor in Europe.

Copulation

Downy

The amount of preliminary activity that preceded copulation in the Downy Woodpecker varied. On May 25, 1940, I was watching the Downys at Nest 1. At 1:28 p.m. the female entered the nest. A minute later the male appeared and perched quietly on a branch near the hole. The female came out of the nest at 1:31 and sat on the branch 10 inches from the male. As far as I was able to determine neither bird had made any sound. The male immediately moved over to the female and mounted her. For several seconds he rapidly fluttered his wings and then remained motionless on the female for 12 to 15 seconds. He then flew away; the female remained motionless on the branch for a minute or two and then entered the nest. At 1:39 the male drummed 8 times about 50 feet from the nest. He stopped, flew over near to the nest and the female came out. She perched on the same branch as before and the male immediately mounted her again. Immediately after copulation the female flew away and the male entered the nest. Nine minutes later he came out of the nest and flew away. At 2:30 he started drumming about 80 feet from the nest and stopped after 15 minutes. The female was on the nest again at 3:10 and left at 4:15. She returned to the nest at 4:28 and went to the hole. The male, who had entered the nest without my knowledge, appeared at the entrance and both birds flew to the same branch as before and again copulated. Immediately after copulation the female flew off into the woods, the male remaining motionless on the branch. After several minutes he too flew away. During copulation this female perched crosswise on the branch. The male reappeared again

at 4:45 and drummed near the nest until 4:54. He then entered the nest and remained inside for 4 minutes. He called several times when he came out, drummed a few times and then flew off into the woods.

On May 11, 1941, I found a female Downy feeding quietly near Nest 7. I heard a Downy drum several hundred feet away; the drumming stopped and almost immediately the male appeared. As the male flew towards the nest the female perched lengthwise on a branch near the nest. She crouched low in readiness for the male and they immediately copulated.

I watched male K drum three or four times near Nest 16 on May 15, 1947. Female M appeared from the woods and they copulated. The female flew off into the woods and several minutes later another Downy female appeared. Male K became very excited and drove the strange female away. Female M then reappeared and she copulated with male K again. Female M again flew away immediately after copulation, her mate remaining near the nest.

I was in the vicinity of Nest 19 on May 16, 1947, when Downy female V perched quietly on a branch just above me. Male T flew past her and alighted on a branch about 15 feet beyond. Female V flew towards the male, spreading her wings and tail to their fullest extent as she fluttered to the branch. She perched about three feet from him and called softly. The male moved over to her and they copulated. Female M and V perched lengthwise on the branch for copulation.

Hairy

Hairy Woodpecker female B was seen feeding quietly in the Southwest Woods on April 24, 1947. At 8:40 a.m. male A, who had left the woods 40 minutes before, returned and called "peenk" once as he entered the woods. Female B flew a little ways towards the male; she flew with her tail spread and a peculiar fluttering of her wings, calling continuously with a soft twittering cry. She perched crosswise on a branch and the male immediately came over to her and they copulated. After copulation the male entered their nest (No. 3) and the female returned to her feeding.

On April 14, 1947, in the same woods I watched female C feeding. She stopped feeding and drummed rather softly several times. Male A who was nearby began to call "peenk" frequently as the female drummed. The female stopped drumming and flew from one tree to the next, gradually working closer to male A. The male called several more times and finally flew over to the female and they copulated. About 10 minutes later the two birds began calling to each other again and finally came close to one another. They appeared about ready to copulate but the male finally flew off into the woods. As will be pointed out later, this was a case of promiscuity since the mate of male A was female B.

Comparison

Drumming may be used by Dendrocopos villosus and D. pubescens as a preliminary action to copulation but generally it is not. D. pubescens perched either crosswise or lengthwise on a branch during copulation but more often crosswise. D. villosus was observed to

perch only crosswise.

Tracy (1933:117) said that the female D. major may express her sexual desire by drumming and that the male does not necessarily respond. Pynnonen (1939:79) stated that either sex of D. major may drum to express sexual desire but that no response from the mate may be received if the mate is physiologically not ready. Tracy (1938: 42) believed that the female D. major gave the initiative for copulation. He stated that the female would drum three times with three taps to each drum. The male when hearing this drum, would immediately fly over to the female and copulation usually followed. The female seemed to have a favorite branch from which she gave the distinctive drum call for copulation. Tracy observed the female to sit crosswise on the branch and usually on a small branch near the top of a tree. I have found no other reference to the distinctive drum call of the female as described by Tracy.

Haverschmidt (1938:9) observed copulation in D. minor. The male would come near the nest and call, whereupon the female would come out of the nest and fly towards the male with a peculiar trembling flight. The females were seen to perch crosswise on the branch when mounted by the males.

The trembling or fluttering of the wings is probably a characteristic action of most species of Dendrocopos when copulation is about to occur. There is apparently much variation in the pattern followed by the members of any one species indicating considerable individual variation.

Promiscuity

Downy

One instance of promiscuity in the Downy Woodpecker was observed. On May 15, 1947, I had just found Downy Nest 16 and was attempting to identify the owners. Male K was drumming nearby and in a few minutes a female appeared and copulated with K. Only partial identification of the female was made but she was thought to be female I. This female was seen later on several occasions in the southeastern and eastern parts of the woodlot in which Nest 16 was situated (Southwest Woods). I assumed that she was the mate of male K until several days later I saw him copulate with female M. It was female M that was later found on the nest and observed feeding the young.

Hairy

On April 14, 1947, I discovered Hairy female C in the Southwest Woods in what I had believed was the territory of male A and female B. Female C was aggressively chasing female B who was offering very little resistance. Female B finally retired deeper into the woods and female C then drummed several times. Male A was nearby all the time watching but not partaking in the struggle between the two females. After female C had drummed, he flew over to her and in a few moments they copulated. They separated and male A flew deeper into the woods in the direction female B had taken. Female C fed quietly for several minutes and then flew south out of the woods towards the trap at the Headquarters House.

Three days later male A and female B copulated in almost the same spot after which I watched the male enter their nest less than 200 feet away.

Within the next three weeks female C was seen several times at my home and at the Headquarters House and once (April 27) as far west as 100 yards beyond the south western corner of the Reserve. She was not seen with a male again. Apparently she was unmated that season; her wanderings indicated that she was not nesting, however, she certainly seemed to have been deliberate in her actions when she courted male A.

Discussion of Drumming

Drumming was used for several different purposes by Dendrocopos villosus and D. pubescens. The pubescens males drummed most actively during the several weeks period just preceding nest construction. The purpose of this drumming may have been two-fold. First, as a courtship "song" or "display," or second, as related to the defense of the nesting territory. Despite the fact that at least three pubescens males wintered in approximately the same area in 1946-1947 (Southwest Woods, males K, U and V), no struggle was observed among them to establish territories. Whatever territorial adjustments were made, they had been completed by the time the females moved from their wintering areas. Also, pair formation was completed before the period of intensive drumming. As far as could be determined, drumming was not an activity associated with pair formation or defense of the nesting territory.

The drumming of the male pubescens is a courtship "song" or "display;" it is an expression of his physiological and psychological state, an expression of his mating desire or readiness. I believe the same to be true for the drumming of the male villosus. The villosus males drummed most actively during the time of nest construction and even the early part of incubation.

Tracy (1933:117) stated that the female D. major may drum to express her sexual desire but that the male does not always respond. Pynnonen (1939:79) believed that if the male did not respond to the

drumming of the female it was because he was not physiologically ready and the reverse was also true. Pynnonen (1939:55) observed an unpaired major male to drum 500 to 600 times in one day and a paired major male to drum 100 to 200 times on the same day. I watched a male pubescens, that was apparently paired, drum 157 times in one hour and three days later 290 times in 45 minutes.

According to Pynnonen (1939:56-59) major stops drumming at the start of nest construction and minor stops drumming when incubation begins. The drumming periods of villosus and minor are similar and the drumming periods of pubescens and major are similar.

Pynnonen (1939:55) found that both major and minor drummed in a territory more extensive than the nesting territory. The chief drumming places of major males were found on the nest tree itself and also as far as 100 meters away. I found the chief drumming place of one villosus male in another woodlot 800 yards from the nest. Although he drummed in one woodlot and nested in another, I believe that both woodlots were part of his nesting territory. Most of the pubescens males were found to drum near the nest, seldom more than 50 feet away.

Pynnonen (1939:60) found that the drumming sometimes stopped entirely during bad weather. The spring of 1947 was unusually cold with much snow, rain and inclement weather and during that year I found far fewer Dendrocopos drumming than during the other years of my study.

Sometimes the birds of a pair called to one another by drumming, especially when they were feeding young in the nest. I found this to be true for both *villosus* and *pubescens*. Many times when I released a *pubescens* from my hand after banding it, the bird would fly into a nearby tree and drum several times.

Nesting Territory Habitat

Downy

The Downy nests in a variety of places. It may choose an orchard, a tree-lined fence row or roadside, in cities or in the country, or in most any woodlot or forested area. Trautman (1940: 290) found that the Downy at Buckeye Lake, Ohio, "...inhabited not only remnant forests but also small woodlands, woodlots, orchards, and solitary rows of trees." Barrows (1912:348) stated that in Michigan "He is a familiar resident not only of the deep forests and smaller patches of outlying woodland, but of nearly every orchard and grove, even coming regularly into the parks and shaded streets of our towns and villages and frequently nesting in such places,..."

The Downy nests on the Reserve were on the edge of woodlots or in relatively open places when within the wooded areas. Saunders (1942:175) described the Downy in Allegany State Park, New York as "...the common woodpecker of the temporary forests,... When it does occur in the climax forest, it is chiefly about the edges, and not far into large forested areas." The Downy nests that G. M. Sutton and I found on the George Reserve are shown on Map 8.

Hairy

The four Hairy nests that I located on the George Reserve were in oak-hickory woods. Two (Nests 1 and 6) were well in from the edge of the woodlot, another (Nest 3) was about fifty feet from

the edge and the last (Nest 4) was on the very edge of a woodlot. These nests are located on Map 9.

Stoner (1932:531) discussing the Lake Oneida region, New York, described the nesting habitat of the Hairy as "Isolated and little frequented woodlands...." Roberts (1939:681) stated that in Minnesota the Hairy "...shows a preference for tamarack and spruce swamps and the wilder stretches of woodlands but does not hesitate to enter city streets and parks, and occasionally nests within the limits of even the larger cities."

Selection of Nest Territory

Downy

The Downy nests on the Reserve were found in the wintering areas of the males. As noted in the discussion of "Pair Formation" the females moved into the wintering territories of the males to nest. On the basis of that evidence, I believe that the male Downy selects the nesting territory.

Hairy

I do not know whether the male or the female Hairy selects the nesting territory. I was able to follow closely the movements of a pair of color-marked Hairys from December, 1946, through the nesting season 1947 (male A, female B, Nest 3). These two birds remained together throughout the winter season and finally nested in one of the woodlots which they had frequented during the winter. In 1948 they nested (Nest 6) in the same woodlot as in 1947 (Nest 3) (see Map 9).

Shelley (1933:204-205) described several of his observations which he believed demonstrated that the female selects the nesting territory. He stated that the male and female kept separate, although adjacent, winter territories and that the nest was always located in the winter territory of the female. None of my observations indicate that the sexes kept separate wintering areas.

Defense of the Nesting Territory

Downy

I observed no action that could be interpreted as defense of a nesting territory by a Downy Woodpecker after nest construction had been completed. Struggles were noted between individuals or between pairs during a period when the birds were presumably seeking nesting sites. This period was one to five weeks before egg laying started.

On April 11, 1942, I came upon four Downys apparently all fighting and soon realized that it was two pairs fighting. One pair was particularly aggressive and tried desperately to drive the other pair away. The first pair finally succeeded in driving the other two birds several hundred feet away where the struggle was abruptly discontinued.

On May 5, 1940, in the Ann Arbor study area four Downys were found in one woodlot. Although there were two males and two females present no definite pairing seemed to exist. All four birds were calling and drumming back and forth to each other and at times all four seemed to be chasing each other indiscriminately. The birds finally flew into another larger woodlot where the struggle soon ceased and each bird apparently went its own way.

My observations indicate that the male defends the nesting territory against other males and his mate defends the nesting territory against other females. In the Ann Arbor area on April 12, 1942, I observed a pair of Downys feeding quietly in a small woodlot. A second male appeared and the first male immediately flew at the intruder to drive him out of the woodlot. The first male, followed closely by

his mate, drove the second male out of the woodlot and into another woodlot 350 feet away. The female remained in the first woodlot, called "peenk" several times after her mate had left, and then returned to her original feeding place. In two minutes a male, presumably her mate, returned and the female called "peenk" several times and gave two rattle calls as he flew into the tree with her.

On May 1, 1940, also in the Ann Arbor area, my attention was drawn to a female Downy loudly calling "peenk." A male was on a tree trunk nearby and seemed to be watching the female. The female continued her calling and flew down close to the male. He became excited and I expectantly awaited some courtship display. However, a second male suddenly appeared and flew straight at the first. The first male hastily flew away closely pursued by the second. The female did not leave her perch and called "peenk" rather softly several times as she watched the chase disappear into the woods. After the males had flown out of sight she began to feed quietly by herself.

Earlier that spring on March 29, again in the Ann Arbor area, I found two females chasing each other. Except for an occasional "peenk" note, neither bird made much noise. A male flew into the tree with the females and idly watched them for a few moments, then flew back down into some cattails where he was feeding. One of the females seemed more aggressive than the other and repeatedly advanced towards the second bird. Sometimes the second bird would allow the first to approach quite close, then both assumed a stiffened posture with the tails spread and the bills pointed skywards. Partially opening and closing her wings rapidly, the first female advanced towards the second.

The second bird responded with a similar wing movement but soon flew into another tree. I watched the two females for nearly 20 minutes and several times I saw the male come up into the trees, watch the females, but take no part in the struggle.

It seems reasonable to suppose that there were some unmated birds about each season. Yet I saw no birds that I believed were unmated by the time egg laying started. Apparently whatever unmated birds there may have been gave up their search for mates early in the nesting cycle, probably a week or more before egg laying started.

Hairy

On April 14, 1947, I found female Hairy C in the Southwest Woods which I believed was the territory of male A and female B. Female C was aggressively chasing female B which finally flew away deeper into the woods. Male A had been watching the struggle and after the departure of female B he copulated with female C.

Female B was unsuccessful in her attempts to drive female C out of the nesting territory. Female C did not break up the pair of male A - female B for they successfully raised a brood there that year (Nest 3). Female C was apparently unmated that year; within the next three weeks she was seen several times at my home and at the Headquarters House and once (April 27) as far west as 100 yards beyond the southwestern corner of the Reserve. The action of female C with male A and female B is described more fully under "Promiscuity."

Selection of Nest Site

Downy

Shelley (Bent, 1939:56) believed that the female Downy selected the nest site. According to his experience "... the female selects the nest site on her winter, or year-round territory." I made no observations that indicated which sex selected the nest site. The drumming activities of the male Downy may be a factor in the selection of the nest site. Downy Nests 6 and 18 were found within 25 feet of the favorite drumming spots of each male. In several other instances the nests were found within a radius of 60 feet of the male's favorite drumming spot.

Hairy

Bent (1939:15) stated "The female probably selects the nesting site...." Shelley (1933:204-205) observed a female Hairy to start and excavate entirely by herself a nest cavity and on the basis of this observation, he believed that the female selected the nest site. Since other observers state that both sexes work at the excavation of the nest, Shelley's observation apparently needs confirmation. I made no observations on this point.

Comparison

Pynnonen (1939:83) believed that it was characteristic for the male woodpecker to select the nest site but that the female sometimes assisted the male. However, he observed that the male of Dendrocopos

major always selected the nest site without any assistance by the female. D. pubescens is apparently much like major for I found that the male pubescens alone selected the nest site.

Nest Site

Downy

I found 13 Downy nests on the George Reserve and all but one were in aspen trees. Eleven were in dead aspens (Populus tremuloides) and one was in a living aspen which was, however, quite rotten in the center. The one nest not in an aspen was located in a piece of a fallen elm (Ulmus sp.) branch caught in a lower branch of the tree about 10 feet from the ground (see Figures 1 and 2). Nine of the nests on the Reserve were in dead stubs which were little more than poles as all the branches had fallen off. Two were in large, spreading aspens that still held most of their branches. Data pertaining to the Downy nests found are summarized in Table 5. The location of the nests on the Reserve is shown on Map 8.

Audubon (1834:81) described the Downy as "...shewing little care as to the kind of tree it selects for the purpose, although it generally chooses a sound one, sometimes, however, taking one that is partially decayed." Other authors note the Downys' preference for decayed trees in which to excavate their nests. Howell (1932:312) stated that in Florida "The nest of the Downy is usually dug in a decaying limb of a tree..." Roberts (1932:684) said in Minnesota "A hole in a live or dead tree, usually the latter; preferably dead willows and poplars..." Macon and Macon (1909:330) recorded the following observations from Canada "(W. Raine) Almost every decayed stub or broken tree contained a nest... (Criddle) All nests found by me near Aweme, Man., were in aspen woods and trees." Grinnell and Miller (1944:243) made an

Explanation of Figures 1 and 2

Views of Downy Woodpecker Nest 16

Figure 1 shows the general location of the nest which is indicated by an arrow.

Figure 2 is a close-up of the nest which is marked with a circle. One of the adult Downys is sticking its head out of the hole.



Figure 2



Figure 1

Table 5

Description of Downy Woodpecker Nest Sites

Nest No.	Height of nest Above Ground	Description of Tree			Year Nest was Found
		Species	Living or Dead	Diameter at Breast Height	
1	14 ft.	Basswood	Dead	18 in.	1940
2	12 "	"	"	16 "	1941
3	35 "	Elm	Living	22 "	1942
4	7 "	Aspen	Dead	12 "	1940
5	12 "	"	"	10 "	1941
6	10 "	"	"	8 "	"
7	22 "	"	"	16 "	"
8	10 "	"	"	12 "	"
9	9 "	"	"	8 "	"
10	11 "	"	"	10 "	1942
11	15 "	"	"	9 "	"
12	20 "	White Oak	"	--	1946
13	30 "	Aspen	"	24 "	"
14	50 "	Oak	Living	--	"
15	15 "	White Oak	Dead	7 "	"
16	8 "	Elm	"	10 "	1947
17	20 "	Aspen	Living	12 "	"
18	18 "	"	Dead	12 "	"
19	38 "	"	"	15 "	"
20	28 "	"	"	24 "	"
21	7 "	---	"	7 "	"

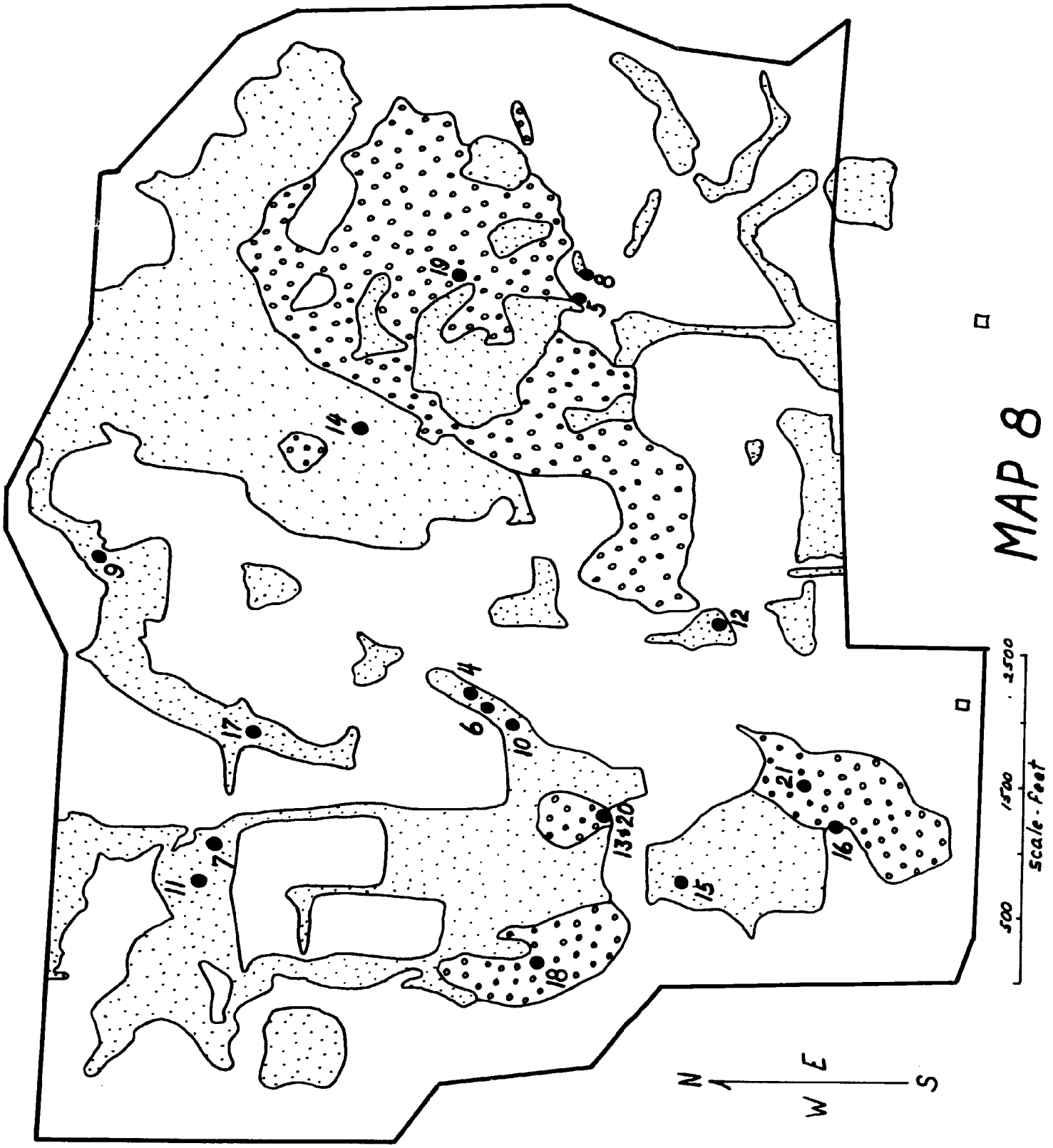
Explanation of Map 8

Location of Downy Woodpecker Nests on the George Reserve

Each nest is indicated by a large solid dot.

The year each nest was found is given in Table 5, and the number by each nest corresponds with the nest number in the table.

Oak-hickory woodlots are stippled, forested swamplands are marked with open dots.


MAP 8
N
E
S
W
500
1500
2500
scale-feet
5
6
7
8
9
10
11
12
13+20
14
15
16
17
18
19
21

interesting comment on the nesting site of the Willow Downy Woodpecker (Dendrocopos pubescens turati) "Thus the lowland stream-bottoms constitute the main theaters of activity of this woodpecker... But there is some invasion of the oak belts locally, even of tracts of conifers; and deciduous orchard trees, notably apple, satisfy the birds' needs. Branches or boles of any of these trees must be far advanced in decay to be excavatable for nest or shelter purposes. Repeatedly, elimination of all such digable wood in a given neighborhood has been observed to be followed by a disappearance of the birds."

The nests on the Reserve varied in height from 7 to 38 feet above the ground, the average height being about 15 feet. Barrows (1912: 349) stated that the Downy placed its nest "...often only two or three feet above the ground." Roberts (1932:684) gave "...from near the ground to 30 or 40 feet.", and Tyler (Bent, 1939:55-56) "...8 feet (rarely less) to 50 feet (rarely more) above the ground." Kumlién and Hollister (1903:75) recorded a Downy nest in Wisconsin that was only 26 inches above the ground.

On the Reserve there did not appear to be a preference for trees of any particular size. Most of the dead aspen stubs there were comparatively small, ranging from 8 to 12 inches in diameter. The diameter of the tree or branch at the nest varied considerably. In many cases it seemed barely large enough to allow for the excavation of the nest, in others the tree or branch was so large that the nest excavation probably did not reach the center.

All the nests discovered by me were new excavations, not nesting cavities of a former year. Also, as far as could be determined, not one of the nests was the enlargement of a winter shelter hole. Shelley (Bent, 1939:56) stated that in Massachusetts a female used her winter shelter hole for the nest the following spring. Studer (1903:27) claimed that the Downy "...always prefers to find, if possible, a hole in which either he or some of his kindred have already reared their young." In New England, Samuels (1867:93) made a similar observation, "I think that the nests of this species, as of some others, are used for successive seasons, as I have found apparently old nests occupied by breeding birds." Recent authors make no reference to the Downy using an old hole for its nest.

A number of the stubs and trees on the Reserve were used for several successive years by the Downys but in each case a new excavation was made. Nests 13 and 20 were built in the same tree, Nest 20 being excavated about two feet below Nest 13 the following year. Knight (1908:275) made a similar observation for the Downy "This same stub had a nest of the species for several previous years, a new hole being excavated each season."

Hairy

The Hairy nests on the George Reserve were all in living trees which were decayed in the center. In 1941, Nest 1 was situated in a tall sassafras (Sassafras albidum); the tree was eleven inches in diameter at breast height and the nest was about 45 feet from the ground. The tree, although living, was rotten in the center. Nest 3

found in 1947 was in a large living red oad (Quercus rubra) (20 inches DBH). The nest was 42 feet 6 inches from the ground and it had been drilled into the first large limb of the tree. This limb projected from the trunk of the tree at an angle of about 40 degrees from the horizontal and the nest hole was on the underside of the limb three and one-half feet from the trunk. The limb, which was about nine inches in diameter at the nest, was living but rotten in the center.

Nest 4, also found in 1947, was in a living red oak about 17 inches in diameter and the nest was approximately 35 feet from the ground. The top of the tree was dead and the nest had been drilled into the main trunk about three feet below the dead portion. Nest 6 found in 1948 was about 55 feet from the ground in a living red oak (20 inches DBH). The nest was inaccessible but the branch in which the nest had been drilled appeared mostly dead and was probably partially decayed.

One Hairy nest in the Ann Arbor study area (Nest 2) was located in a small woodlot of about three acres in size. The nest, which was only six feet from the ground, was in a dead basswood (Tilia americana) stub 16 inches in diameter and only seven feet high. Data pertaining to the nests found are summarized in Table 6. The location of the nests on the Reserve is shown on Map 9. Figures 3 and 4 are photographs of Nests 1 and 3.

Sutton (1928:142) found that in the Pymatuning Swamp, Pennsylvania, the Hairy nests "... were drilled near the tops of dead trees which nearly always stood in water." The 26 nests he noted there averaged 30 feet from the ground. Roberts (1932:681) noted that in Minnesota the Hairy nests were "... in either living or dead trees, usually the

Table 6

Description of Hairy Woodpecker Nest Sites

Nest No.	Height Above Ground	Description of Tree			Year Nest Was Found
		Species	Living or Dead	Diameter at Breast Height	
1	45 ft.	Sassafras	Living	11 inches	1941
2*	6 ft.	Basswood	Dead	16 "	1942
3	42 1/2Ft.	Red Oak	Living	20 "	1947
4	35 ft.	Red Oak	Living	17 "	1947
6	55 ft.	Red Oak	Living	20 "	1948

* found in the Ann Arbor study area, all others were found on the George Reserve.

Explanation of Figures 3 and 4

Views of Hairy Woodpecker Nests 1 and 3

Figure 3. Nest 1 in the Southwest Woods in 1941. The nest is indicated by the circle.

Figure 4. Nest 3 in the Southwest Woods in 1947. The nest, indicated by the arrow, is on the underside of the branch. The photograph was taken from inside of the blind.



Figure 4



Figure 3

Explanation of Map 9

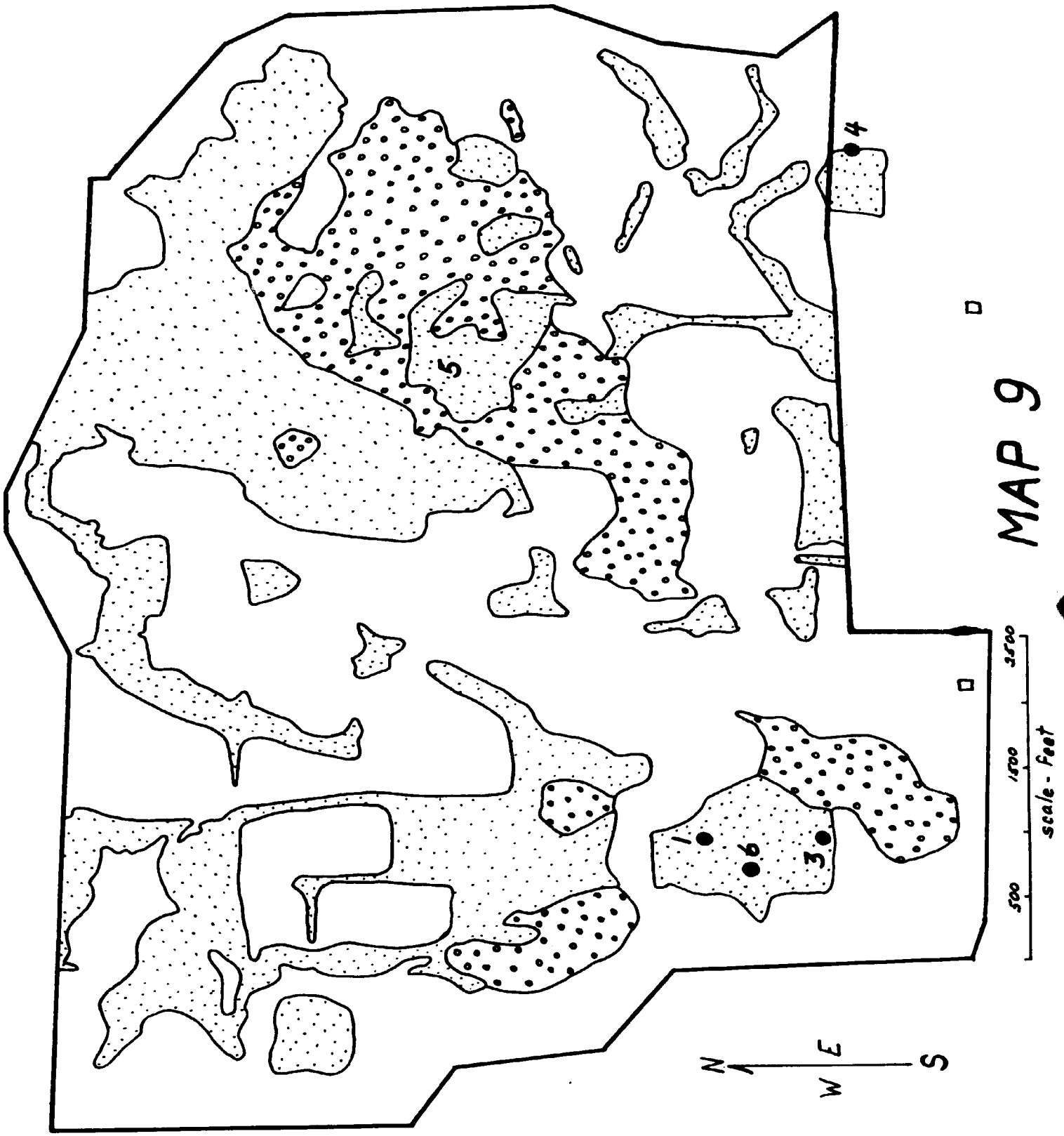
Location of Hairy Woodpecker Nests on the George Reserve

Each nest is located by a large solid dot.

The year each nest was found is given in Table 6, and the number by each nest corresponds with that in the table.

The nest of Pair 5 was not discovered. It was thought to be within the area enclosed by the broken line.

Oak-hickory woods are stippled areas, the forested swamplands, largely tamarack, are marked with open dots.



MAP 9

latter." In the Lake Oneida region, New York, the Hairy (Stoner, 1932: 531) "...usually chooses a nesting site well up in a dead or dying maple, beech or other forest tree."

Concerning the Hairy in Michigan, Barrows (1912:346) stated "The nest is ... in the dead wood of a trunk or limb, usually at some little height above the ground. In some regions maple seems to be preferred, but nests are often found in willow, poplar, and other soft wood trees."

J. C. Wood (1905:66) reported four nests near Detroit in Wayne County, Michigan. The first nest was 50 feet above the ground in a dead elm, the second 55 feet above the ground in a dead beech, the third 15 feet above the ground in a poplar stub, and the fourth 40 feet above the ground in a living beech.

Each woodlot in which I found a Hairy nest also had one or more Downy nests. No conflict between the Hairy and Downy for nesting territories or nest sites was observed. The Hairy nests on the Reserve were in sites quite unlike those of the Downy. The Hairy nests were in large living trees and a considerable height above the ground. The Downy nests were in smaller dead trees and not nearly as high as the Hairy nests. Examination of Tables 5 and 6 will show these differences.

It would seem that the earlier nesting of the Hairy lessened the possibility of conflict between the species when selecting a nest site. The Hairy usually had its nest constructed and incubation in progress before the Downy began the construction of its nest. In the Ann Arbor study area Hairy Nest 2 was in a site where I would have expected to find the nest of a Downy, and Downy Nest 3 was in a dead branch of a

live elm tree about 100 feet away, These two nests were in a woodlot of about five acres. The Hairy nest had two small young. Judging by the actions of the Downys at their nest, which was inaccessible, incubation was in progress.

Several more extensive woodlots were nearby. Although other pairs of Downys and possibly one other pair of Hairys nested in the general area, no evidence was noted of population pressure, lack of nesting sites, or any other factor that may have compelled the two pairs to nest so close together and in such a small woodlot.

Nest Construction

Downy

On the George Reserve both the male and female Downy worked at excavating the nest. Most of the Downy nests on the Reserve were in rotten stubs or in other situations that made them inaccessible to me. I was able to watch the progress of the construction of a nest found in 1940 (Nest 4). When found on the morning of May 24 the entrance had been completed and the birds were working on the downward enlargement of the cavity. It was necessary for the laboring bird to back out of the hole, for apparently the cavity was still so small that the Downy could not go inside to turn around. By the following morning the downward excavation of the cavity, which was now about 3 inches in depth, had progressed considerably and the Downy was able to leave the nest head first. On May 29 the birds were still working on the nest but it appeared practically completed and the cavity was about 8 1/2 inches deep.

The male and female worked alternately excavating this nest, each bird working about 20 minutes before being relieved by the other. On one occasion the female interrupted her labor and fed in the nearby trees for 10 minutes, then returned to work on the nest. Before working in the nest cavity each bird first spent several minutes throwing chips out of the nest to the ground below. Each bird stopped excavating occasionally and threw out some chips but apparently they allowed most of the chips to remain in the nest and the next bird to work would have to throw them out before excavating.

A male Downy had been observed drumming on a certain dead tree near the above nest on May 10, 13, 17, and 20. Although he was not marked, I presume that it was the same male that eventually nested there. After nest construction had started, he apparently ceased his drumming, for I did not hear him drum again until on May 29 when the nest was completed.

Downys were observed working at five other nests and at all both sexes worked at the excavating. Tyler (Bent, 1939:56-57) described the behavior of a pair working together on a nest at Ithaca, New York. The early investigators like Audubon (1834:81) and Wilson and Bonaparte (1831:162) also stated that both sexes worked at constructing the nest. Shelley (Bent, 1939:56) seems to be the only observer to state that one sex excavates the nest. He stated "Of a number of nests observed, I have never known the male downy to assist in excavating. He often comes near when the female is working, but this seems to be an understood signal for her to cease work and go off in his company."

At the nests where I observed the birds working, they all threw the chips to the ground from the nest. At the other nests found by me, sixteen in all, I noted chips on the ground beneath the nest. On occasion some of the chips may be carried away, for DuBois (Bent, 1939:56) saw the female carry a bill full of chips away instead of tossing them to the ground from the nest as had been her habit. Wilson and Bonaparte (1831:162), who believed that the male did most of the excavating, said that the Downy carefully carried away the chips.

Tyler (Bent, 1939:56) has desc ibed the nest of the Downy as follows: "The entrance, one and a quarter inches in diameter, is just large enough to admit the bird's body,...". The cavity is roughly gourd-shaped, turning downward and widening soon after penetrating the wood and extends to a depth varying normally from eight to twelve inches."

Hairy

Recent authors, with the exception of Shelley, state that both sexes of the Hairy Woodpecker work at excavating the nest. Shelley (1933:204) believed that the female constructed the nest alone. Bent (1939:15) noted that "This work requires one to three weeks, depending on how hard the wood is; a cavity in the soft wood of a poplar, which is a favorite with the species in some localities, might be excavated in a very short time, but I have known a pair to take over three weeks to excavate a nest in a hard maple;..."

At the five nest I found, fresh chips were on the ground beneath each one. "A new nest may often be recognized by the presence of fresh chips on the ground around the tree, as the birds are not very particular about removing them." (Bent, 1939:15). Knight (1908: 273-274) observed a pair of Hairys working at their nest near West Oldtown, Maine, where he watched the excavating bird appear at the entrance of the nest with a bill full of chips, transfer them to the bill of the mate outside the nest who in turn flew away with them.

Cahn (1913:129) said that the Hairy in Wisconsin returned "... year after year to the same hole if left undisturbed." Bent (1939:15)

stated "Usually a fresh hole is made each season, but I have seen occupied holes that were very much weathered, as if they had been occupied for more than one season;..." I found no evidence that the birds used old holes for their nests and know of no positive report in the literature of such an occurrence. The Hairy may prove to nest in old holes on rare occasions for in Montana, Weydemeyer and Weydemeyer (1928:342) said they found one nest of D. v. septentrionalis in a woodpecker nesting box. A. L. Rand of the Chicago Natural History Museum sent me data filed there on the nest measurements of five Hairy nests. Their measurements are listed below.

Diameter of Hole	Depth of Nest	Inside Diameter	Locality
1 5/6 in.	11 3/4 in.	3 1/2 in.	Iowa
----	12 in.	--------	Mass.
----	12 in.	--------	Mass.
2 x 1 7/8 in.	10 in.	4 1/4 in.	Iowa
2 in.	8 in.	---------	Missouri

Egg Laying

Downy

I was unable to make any observations on the time required by the Downy to lay its eggs. Trautman (1940:290-291) at Buckeye Lake, Ohio, made observations at a Downy nest that enable one to estimate the time required to lay the eggs. Additional information about this nest was supplied me by Trautman in a letter.

Between 5:30 and 6:30 a.m. on May 8, 1931, Trautman examined a Downy nest, flushing a female from it as he did so. He stated in his letter that "Looking into the cavity I saw no eggs and feel confident there were none." On May 20 there were five eggs and on May 29 four small young.

In the evening of June 13, Trautman again examined the nest. The wire fence upon which he was climbing to reach the nest broke, thus creating considerable disturbance. The confusion apparently frightened the young birds for they suddenly left the nest. "...the young were out of the nest and clinging to the branches of nearby trees."

If we assume that the young were about ready to leave the nest on June 13, then they were 19 or 20 days old for that is the age at which young Downys leave the nest. The young presumably hatched on May 25 or 26. As the incubation period is stated to be 12 days then incubation started on May 13 or 14. This would leave five or six days during which the female could have laid the five eggs.

Comparison

I have been unable to find any information about the egg-laying of Dendrocopos villosus. In Finland, Pynnonen (1939:109) reported that D. major and D. minor laid one egg daily until the clutch was complete. The egg-laying of these two species usually occured in the morning. K. Loos (Pynnonen, 1939:109) stated that Dryocopus martius of Europe lays one egg daily and the same has been found of Colaptes auratus in North America (Bent, 1939:272). From Trautman's observation described above under D. pubescens I concluded that the female laid the five eggs in five or six days. On the basis of the data known from other species of woodpeckers, it is probably correct to assume that, in Trautman's observation, the eggs were laid daily.

Description of the Eggs

Downy

The excellent description of the eggs of the Downy Woodpecker as given by Bent (1939:57) is quoted here. "The eggs are pure white, either dull white or more or less glossy, and they vary in shape from ovate to rounded-ovate. The measurement of 55 eggs average 19.35 by 15.05 millimeters; the eggs showing the four extremes measure 22.35 by 16.26, 17.78 by 14.73, and 18.80 by 13.97 millimeters."

Hairy

Bent's (1939:15-16) description of the Hairy's eggs is quoted here. "The eggs vary in shape from oval to elliptical-oval, usually more nearly oval. The shell is smooth and often quite glossy. The color is pure white, but in fresh eggs the yolk shows through the translucent shell, giving the egg a beautiful orange-pink color. The measurements of 47 eggs average 23.81 by 18.04 millimeters; the eggs showing the four extremes measure 29.50 by 18.80, 28.70 by 18.90, and 20.57 by 16.26 millimeters."

Clutch Size

Downy

Barrows (1912:349) stated that the Downy lays four or five eggs and three or six are not rare; Wilson and Bonaparte (1831:163) gave six as the usual number; Roberts (1932:684) and Stoner (1932:532) both said four to six; Bent (1939:59) gave the same figures as Barrows, adding that seven or eight eggs in a nest have been found.

My own data are insufficient to determine accurately the average number of eggs laid by the Downy. To these data I have added ten records from Michigan, five from New Jersey, and one from Ohio.

Number of Eggs	Locality	Authority
6	Mich: George Reserve	Staebler
4	" " "	"
5	" Washtenaw Co.	J.W.Harris (Univ.Mich.Mus.Zool.)
5	" Oakland Co.	F.C.Hubel " " " "
5	" Kalamazoo Co.	Westnedge (1891:6)
5	" " "	" "
7	" " "	" "
4	" " "	Rapp (1931:16)
6	" Wayne Co.	B.H. Swales' notes
5	" " "	" "
6	New Jersey: Cape May	Stone (1937:668)
5	" " " "	" "
5	" " " "	" "
3	" " " "	" "
5	" " " "	" "
5	Ohio: Buckeye Lake	Trautman (1940:290)

In 16 nests, 81 eggs were laid, an average of 5.06 eggs per nest.

Hairy

I discovered only one Hairy nest before the young hatched. No attempt was made to determine the number of eggs, which could have been accomplished only by cutting a hole into the nest, for fear of causing the birds to desert. In the literature are three records of nests with eggs from Michigan. There also is a set of eggs collected in Michigan in the Colorado Museum of Natural History. To these Michigan records I have added one each from Ohio and New Jersey and seven records of the Chicago Natural History Museum, the data of which were furnished by A. L. Rand.

Number of Eggs	Locality	Authority
5	Mich: Kalamazoo Co.	Rapp (1931:15)
4	" Wayne Co.	Purdy (1889:93)
4	" " "	J.C.Wood (1905:66)
4	" Genesee Co.	A.W.Plumb (Colo.Mus.Nat.Hist.)
5	Ohio: Buckeye Lake	Trautman (1940:289)
4	New Jersey: Cape May	Stone (1937:666)
4	Iowa: Kossuth Co.	W.H.Bingaman (Chi.Nat.Hist.Mus.)
4	" " "	" " " " "
4	" Johnson Co.	Paul Bantal " " " "
5	Missouri: Jackson Co.	P.W.Smith, Jr. " " " "
2	Illinois: Marshall Co.	R.M.Barnes " " " "
4	Conn: Fairfield Co.	H.W.Beers " " " "
3	Mass: Middlesex Co.	E.S.Coombs " " " "

A total of 52 eggs was laid in 13 nests or an average of 4 eggs per nest.

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4	" Johnson Co.	Paul Bantal " " " "
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3	Mass: Middlesex Co.	E.S.Coombs " " " "

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Comparison

Dendrocopos villosus averages about one egg less per nest than *D. pubescens*. In Europe, *D. leucotos* lays 3 to 5 eggs (Niethammer, 1938:21), *D. minor* lays 5 to 6 (1938:25) and *D. major* lays 4 to 8, mostly 6 (1938:16). *D. leucotos* is the first of the European species to nest in the spring and is followed by *D. minor* which in turn is followed by *D. major*. It is interesting to note that the first species to nest in America and Europe lays fewer eggs per nest than do its close relatives that nest later in the season.

Incubation

Downy

According to Burns (1915:283) the incubation period of the Downy Woodpecker is 12 days. There is no indication of the source of Burns' information, but no more satisfactory report was found.

The duties of incubation are shared by both sexes of the Downy. On numerous occasions male or female Downys were flushed from their nests, each with equal frequency. Butler (1898:833) said that in Indiana "Both sexes incubate,..."

I made several attempts to secure data on the incubation habits of the Downy but had very little success. The birds replaced each other at the nest very quietly, so that unless I was watching constantly the entrance of the nest I failed to see the relieving of one bird by the other. On the morning of June 14, 1947, from 6:00 a.m. to 8:40 a.m. some observations were made at one nest. During a period of two hours and forty minutes the male incubated the eggs for a total of 104 minutes. The female incubated the eggs for somewhat less than 56 minutes. Her departure from the nest before the arrival of the male at 7:07 was not observed but apparently it was ten minutes or less before the male arrived.

On one occasion I noted the male incubating the eggs on a nest at 8:30 p.m. (May 26) and presume that he remained on the nest all night. Skutch (1933:437) reported that in Guatemala the males of four different species of woodpeckers incubated the eggs at night.

Incubation by the Downy seems to start before the last egg is laid. At one nest the young hatched over a period of two or two

and one-half days. The young that I banded in four nests were, in each nest, all of equal size and development, although in one case one of the four young remained in the nest one day longer than the others.

Hairy

According to Burns (1915:283) the incubation period of the Hairy is 14 days. There is no indication of the source of Burns' information, but no more satisfactory report is known to me.

Although I was unable to make any direct observations on incubation by the Hairy, the development of the young studied indicated that incubation may sometimes start before all of the eggs are laid. All the young (three or four) left one nest on the same day while at another nest two of three young left the nest four days before the third young. The young in this last mentioned nest were banded about a week before they left and at the time of banding the difference in their degree of development was noticeable.

The duties of incubation are shared by the two sexes. Study of other species of woodpeckers has shown that both sexes incubate. In Guatemala, Skutch (1933:437) found that the males of four different species of woodpeckers including Dendrocopos villosus sanctorum incubated the eggs at night. Butler (1898:831), referring to the Hairy in Indiana, stated: "Both birds assist in incubation,..."

I had one nest under observation during the incubation period. Both birds of this pair were color-banded and on several occasions

the male or the female was seen. I assume that the other parent was incubating the eggs under these circumstances. The only possible manner in which the incubating bird could be flushed from this particular nest was to climb the tree. Pounding on the trunk would not cause the incubating parent to leave. At Buckeye Lake, Ohio, Trautman (1940:289) had the same difficulty for he stated: "To locate the nests was rather difficult, for unlike most birds which nest in tree cavities, this species could not be flushed from its nest by pounding on the base of the tree with a hammer or log. To flush the incubating bird it was necessary to climb the tree suspected of containing a nest and reach into the nesting cavity with the hand or a stick."

Comparison

The incubation activities of Dendrocopos villosus and D. pubescens and also of the four species of Dendrocopos in Europe are apparently all very similar. Both sexes in D. major, minor, and medius (Niethammer, 1938), and leucotos (Pynnonen, 1939:115) are known to incubate the eggs. In all of these species the male is reported to incubate at night. Niethammer (1938:16) has stated that incubation in D. major sometimes starts before the last egg is laid. This was true for D. pubescens and possibly also for D. villosus.

The incubation period of D. minor is 14 days (Niethammer, 1938: 25; Witherby, 1938:290). That of D. major is noted as 12 days by Niethammer (1938:16) and Pynnonen (1939:112) although Witherby (1939: 285-286) gave 16 days for the incubation period. Pynnonen studied the nesting habits of D. major in considerable detail and his findings

of 12 days may be accepted as the more accurate. It is interesting to note that the larger species, D. major, has a shorter incubation period than the smaller species D. minor. D. minor nests from one to two weeks earlier than D. major; in this country the larger species, D. villosus nests one to three weeks before the smaller species, D. pubescens. According to the information on hand the earlier nesting species in each case has the longer incubation period.

Removal of Egg Shells and Infertile Eggs

Two days after the last young in Downy Nest 16 had hatched, the 3 presumably infertile eggs and the shells from the hatched eggs were still in the nest. On the following day (June 2) the three infertile eggs were gone although most of the shells were still in the nest. Five days after hatching (June 4) most of the shells had been removed but one nearly complete shell still remained. On June 5 I found that the nest had been destroyed by some predator.

It seems strange that the infertile eggs should have been removed before the empty egg shells. I made certain on June 2 that there were no eggs in the nest. The chips in the bottom of the nest were dry and clean. I therefore concluded that the infertile eggs had been removed intact and that the remaining shells in the nest were from the eggs that had hatched.

When I banded the young in Downy Nest 17 I looked in the bottom of the nest for remains of egg shells and found a number of small pieces, none larger than four or five millimeters square. These young were about 18 days old when banded. The Downy apparently does not remove all of the egg shells but allows some of them to remain in the nest.

Number of Young in the Nest

Downy

I was unable to secure sufficient data to determine the hatching success of the eggs or mortality of the young in the nest.

Below are listed 24 nest records in which the number of young were known. The number of young were determined in 8 nests on the George Reserve--three by G. M. Sutton and five by me. I have added 15 additional records from Michigan and Ohio.

Number of Young	Locality		Authority
6	Mich:	George Reserve	Staebler, Nest 7
5	"	" "	" " 6
3	"	" "	" " 12
3	"	" "	" " 16
4	"	" "	" " 17
3	"	" "	G.M. Sutton
4	"	" "	"
6	"	" "	"
5	"	Dickinson Co.	Gaige (1914:81)
4	"	Kalamazoo Co.	Westnedge (1891:6)
4	"	Wayne Co.	B.H. Swales notes
2 nests with 3	Ohio:	Buckeye Lake	Trautman (1940:290-291)
5 " " 4	"	" "	" "
6 " " 5	"	" "	" "

In 24 nests there were 97 young, or an average of 4.04 young per nest.

Hairy

I determined the number of young in three of the four Hairy nests found by me. To these records are added one other Michigan record and one each from Ohio and New Jersey. The six records are listed below.

Number of Young	Locality	Authority
2	Mich: George Reserve	Staebler, Nest 2
3	" " "	" " 3
4	" " "	" " 4
3	" Luce Co.	O. M. Bryens
3	New Jersey: Cape May	Stone (1937:666)
4	Ohio: Buckeye Lake	Trautman (1940:289)
4	Illinois: Marshall Co.	Chi.Nat.Hist.Mus.

In the seven nests a total of 23 young was found, or an average of 3.3 young per nest.

Comparison

The average number of young in the nest of Dendrocopos pubescens is one less than the average number of eggs in the nest, that is to day, 4.04 young per nest as compared to 5.03 eggs per nest. The average number of young per nest for D. villosus is 3.3 as compared to an average of 4 eggs per nest. In Finland, Pynnonen (1939:110) found that D. major averaged one less young than eggs per nest, 4.8 young as compared to 5.7 eggs.

Brooding of the Young

Downy

Temperature seems to be an important factor in determining the amount of brooding required by nestling Downys. If the air temperature is high nestlings that are three days old or older are brooded very little or not at all. However, during cold weather, nestlings as old as nine days are frequently brooded.

I did not carry a thermometer with me while in the field. With the exception of the data of some individual workers, no temperature records have been kept on the George Reserve. Meterologist H. M. Wills, Director of the Michigan Section of the U. S. Weather Bureau at East Lansing, Michigan, has informed me that there is very little variation between the temperature extremes of Ann Arbor and East Lansing. As the George Reserve lies about midway between these two localities, an average of the two readings has been used here when the variation was more than three degrees, otherwise the readings of East Lansing were used. Mr. Wills supplied me with temperature data for Ann Arbor and East Lansing for those days for which I needed that information.

Nestlings that were two days old were brooded about 50 per cent of the time on May 22, 1941, when the temperature was about 80°F. (Nest 7). On May 25, 1941, the temperature varied from 65° to 72°F. during the period of observation and the three-day-old young (Nest 6) were brooded 60 per cent of the time. However, at Nest 9 the three-day-old nestlings were not brooded at all, the temperature that day (May 28, 1941) being about 84°F. Five-day-old young were brooded

almost constantly, 95 per cent of the time, at Nest 17 on June 22, 1947. This was an uncomfortably cool day for late June (55° to 60°F.) and a strong east wind blew almost directly into the nest hole. It was cold (61° to 65°F.) and raining on June 30, 1947, and the nine-day-old nestlings at Nest 17 were brooded about 40 per cent of the time. I did not observe brooding of the young more than nine days old under any weather conditions.

The male and female Downys divided the duties of brooding equally. The males were observed to brood the young a total of 215 minutes and the females a total of 220 minutes. The longest single brooding-period was by a male on June 22, 1947; he remained on the nest 50 minutes. The average amount of time spent brooding was ten minutes for each period. The above data are presented graphically in Figure 5.

Sometimes the nestlings were left unattended for rather long periods of time. Two-day-old young were left unattended for a maximum period of 14 minutes, three-day-old young for 25 minutes and five-day-old young for a maximum of 40 minutes.

The total amount of time each parent brooded the nestlings during any given observation period varied. For example, at Nest 7 on May 22, 1941, the female brooded the two-day-old young 80 per cent of the total amount of time they were brooded during the period of observation that day, although on May 25 when these young were five days old, the female performed only 25 per cent of the total brooding during the observation period (see Figure 5). At a nest on June 22, 1947, 60 per cent of the brooding performed during the observation

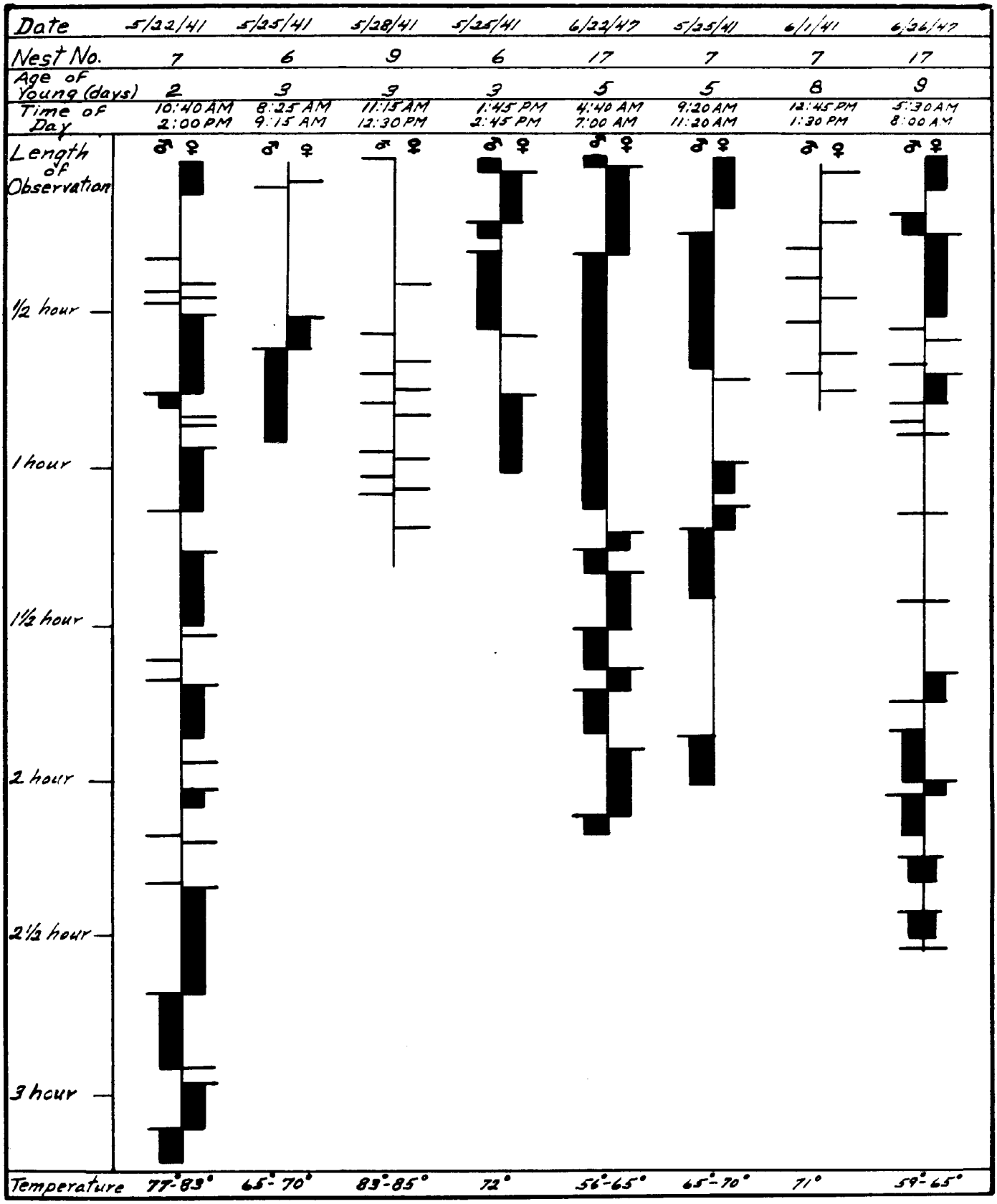
Explanation of Figure 5

Brooding of Young by Adult Downy Woodpeckers

The period of observation at each nest is indicated by the vertical lines. The visit of an adult to the nest is shown by a short horizontal line; a line to the left of the vertical line indicates the male, to the right the female; and a line crossing the vertical means the sex of the visiting bird was not determined.

The parents entered the nest at each visit and the length of time they spent in the nest is indicated by the solid blocks.

FIGURE 5


Date
5/22/41
5/25/41
5/28/41
5/25/41
6/22/47
5/25/41
6/1/41
6/26/47
Nest No.
7
6
9
6
17
7
7
17
Age of Young (days)
2
3
3
3
5
5
8
9
Time of Day
10:40 AM
2:00 PM
8:25 AM
9:15 AM
11:15 AM
12:30 PM
1:45 PM
2:45 PM
4:40 AM
7:00 AM
9:20 AM
11:20 AM
12:45 PM
1:30 PM
5:30 AM
8:00 AM
Length of Observation
♂ ♀
1/2 hour
1 hour
1 1/2 hour
2 hour
2 1/2 hour
3 hour
Temperature
77°-83°
65°-70°
83°-85°
72°
56°-65°
65°-70°
71°
59°-65°

period was done by the male and at the same nest on June 26 the condition was quite the opposite for 60 per cent of the brooding was done by the female.

On June 30, 1947 (see Figure 5) the last feeding of the young for the day was by the male at 8:05 p.m., 13 minutes before sunset. The male remained inside of the nest after that feeding. On the morning of July 3, 1947, the above male did not leave the nest until 5:20 a.m., 18 minutes after sunrise. At another nest the male was flushed from his nest which had three young four days old at 4:30 a.m. on June 3, 1947.

There was a fairly definite pattern followed by the parents when exchanging positions at the nest during the brooding period. The arriving bird would call softly two or three times as it approached the nest and perch a few feet away. If the brooding parent did not come out of the nest immediately, the arriving parent would fly to the entrance and call softly again and occasionally look into the nest. After departure of the brooding parent the other immediately entered. Sometimes the parent did not remain in the nest to brood the young but left immediately or before its mate arrived. On these occasions when the other parent arrived at the nest it would, after failing to arouse its mate (supposedly in the nest), peer anxiously into the nest several times and, after hesitating several minutes, finally enter.

Hairy

From the start of feeding activities in the morning, about 5:15 a.m., to 10:00 a.m., the nestling Hairys less than six days old were brooded almost constantly, about 90 per cent of the time. At nine days of age they were brooded about 75 per cent of the time and at the age of 12 days they were no longer brooded during the cool morning hours. The duties of brooding were shared equally by both sexes. The average length of stay in the nest was slightly less than 10 minutes and varied from one to 44 minutes. The small young were left unattended for short periods of one to six minutes. The brooding of the nestling Hairys is depicted in the graph in Figure 6.

There was a fairly definite pattern followed by the parents when exchanging positions at the nest during the brooding periods. The arriving parent would call softly two or three times as it approached the nest or lit a few feet away from the nest entrance. If the brooding parent did not come out immediately, the arriving parent would fly to the entrance and again call softly and sometimes look into the nest. After the departure of the brooding bird, the other immediately entered. Sometimes the parent did not remain in the nest to brood the young after feeding them, but left the nest. On these occasions when the other parent arrived at the nest it would after failing to arouse its mate supposedly in the nest, peer anxiously into the nest several times and after hesitating several moments, finally enter. I never saw the two adults in the nest together.

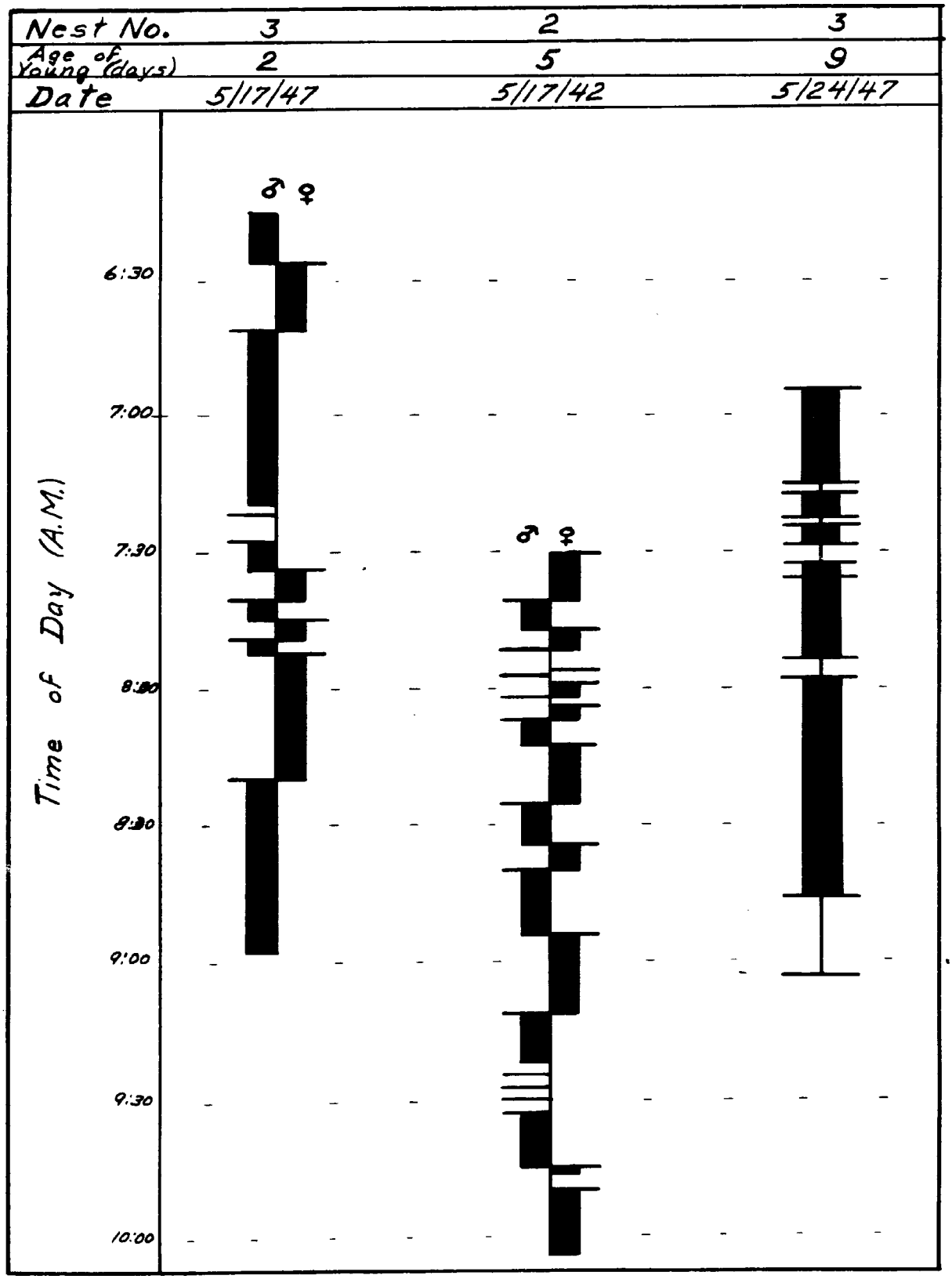
Explanation of Figure 6

Brooding of Young by Adult Hairy Woodpeckers

The period of observation at each nest is indicated by the vertical lines. The visit of an adult to the nest is shown by a short horizontal line; a line to the left of the vertical line indicates the male, to the right the female; and a line crossing the vertical means the sex of the visiting bird was not determined.

The parents entered the nest at each visit and the length of time they spent in the nest is indicated by the solid blocks.

FIGURE 6


Nest No. 3 2 3
Age of Young (days) 2 5 9
Date 5/17/47 5/17/42 5/24/47
♂ ♀
♂ ♀
6:30
7:00
7:30
8:30
8:30
9:00
9:30
10:00
Time of Day (A.M.)

An unusual behavior of a brooding bird was noted on May 24, 1947, at Nest 3. One of the parents entered the nest at 7:55 a.m. the other parent was slow in returning to the nest and the brooding bird apparently became uneasy. At 8:37 I heard the bird in the nest drum softly several times followed by three or four loud pecks. A moment later the parent stuck its head out of the nest hole and finally left the nest at 8:39, calling "peenk" several times as it departed.

The male Hairy apparently brooded the young at night. On May 26, 1947, a male Hairy entered his nest to brood the young for the night at 7:53 p.m., nine minutes before sunset. I heard him peck several times on the inside of the nest at 8:15 but from then until 8:50 when I left no other sounds were heard. On the following morning the first sound I heard from the nest was a definite pecking from the inside at 5:01. At 5:04, exactly at sunrise, the male came out and silently flew away. The young were 12 days old at the time. On the morning of May 31 at the same nest the first sounds were several muffled cries of the young, immediately followed by some pecking from inside of the nest. Two minutes later at 5:07 (sunrise was at 5:05) the male silently left the nest.

Comparison

For those species of Dendrocopos for which information has been secured, the male broods the young at night and both sexes share the day-time duty of brooding. (D. major, minor, leucotos in Europe; D. villosus, pubescens, arizonae, and nuttalli in this country.) The females probably spend the night with the young occasionally, for

Pymnonen (1939:135) twice observed a major female and once a minor female to spend the night with the young. Bussman (1946:148) stated that the young of D. major were brooded only rarely after the young were 12 days old.

Feeding of the Young

Downy

Until the young Downys were about two weeks old, the male and female made about an equal number of trips to the nest with food. However, after the young were 14 or 15 days of age, the female fed the young much less than the male and not at all during the last few days that the young were in the nest. For the nesting period as a whole, the young were fed 67 per cent of the time by the male and 33 per cent of the time by the female.

The young were fed on the average about six times per hour, but intervals of 20 to 30 minutes when neither parent brought food were noted a number of times. On one occasion the young were not fed for 68 minutes and on another occasion 54 minutes elapsed between feedings. The frequency of the feedings did not seem to be correlated with the age or the number of young in the nest.

I determined the start of the feeding activities on three different occasions (see Figure 7). On two mornings (June 22, 1947 and June 26, 1947) feeding started at 4:51 and 4:58; sunrise each morning was 4:58 and 5:00 respectively. On July 3, 1947, the morning was clear but cold (52°F.) for that time of the year and feeding did not start until 5:26, or 24 minutes after sunrise. On June 22 the male, who had brooded the young during the night, did not leave the nest until the female arrived with food. However, on June 26 and July 3 the male left the nest before the female arrived and he was the first to bring food to the young in the morning.

On June 30, 1947, a male Downy brought a very large larva for the young who were 13 days old. He tried to give the larva to the young who were clinging to the inner wall of the nest just inside the entrance but he was unsuccessful even after several attempts. He then entered the nest but came out again with the larva still in his bill. He shifted the position of the larva in his bill and returned to the nest and finally succeeded in feeding it to one of the young.

A little later in the day at this same nest just as the male was about to feed the young the female arrived with food. The male shifted to one side of the entrance and the female alighted at the entrance and immediately started to feed the young. Before she had given any of the food to the young the male moved towards her in a threatening manner and drove her away from the entrance. The male then fed the young and after he had left the female returned to the nest and gave the food she had to the young. Thereafter I never saw the female alight near the entrance of the nest while the male was there, instead she would wait on some branch five to fifteen feet away and come to the nest only after the male had left.

On July 3, I again visited this nest and during my period of observation the female came to the nest only occasionally (see Figure 7) and she brought only a small amount of food at each trip. In fact, she seemed to have lost much of her interest in the nest. This may have been a result of the aggressive and domineering manner of the male.

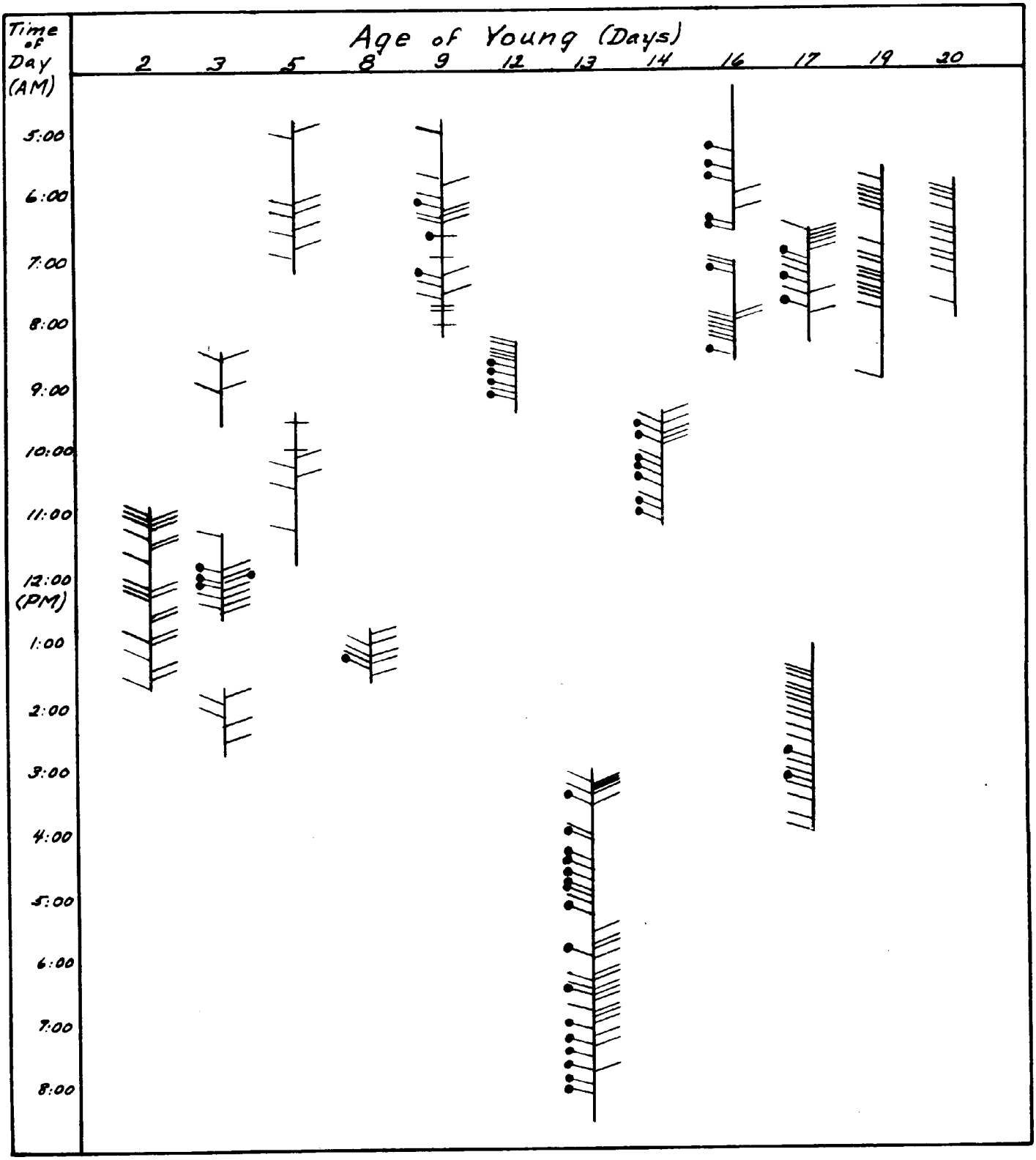
Explanation of Figure 7

Feeding of the Young and Nest Sanitation by the Downy Woodpecker

The period of observation at each nest is indicated by the vertical lines. The visit of an adult to the nest to feed the young is indicated by a short line to the right or left of the vertical line. A short line to the left of the vertical indicates a visit by the male, to the right by the female, and a short line across the vertical indicates that the sex of the visiting bird was not determined.

The solid black dots at the end of some of the short lines indicate that the parent removed fecal material during its visit to the nest.

FIGURE 7


Time of Day (AM)
Age of Young (Days)
2
3
5
8
9
12
13
14
16
17
19
20
5:00
6:00
7:00
8:00
9:00
10:00
11:00
12:00 (PM)
1:00
2:00
3:00
4:00
5:00
6:00
7:00
8:00

Hairy

The female Hairy fed the young a little more often than the male and during the last few days that the young were in the nest she fed them almost alone. Throughout the nestling period of the young, the male fed them slightly less than 40 per cent of the time and the female a little more than 60 per cent of the time.

The young were fed on an average of seven times per hour. Several times the young were not fed for periods of one hour, and once, (May 14, 1947), the young were not fed for 75 minutes. It would appear from Figure 8 that the small nestlings are fed less frequently than are the older young.

The start of feeding activities was determined on three mornings (see Figure 8). On each occasion the first parent to come with food was the female. She arrived at the nest at 5:08 or four minutes after sunrise (May 27, 1947), 5:10 or nine minutes after sunrise (May 31, 1947) and 5:23 or 23 minutes after sunrise (June 3, 1947). In each instance the male had brooded the young at night and he left the nest within one or two minutes after sunrise and 3 to 22 minutes before the female arrived.

Comparison

My observations show that the male and female of Dendrocopos villosus shared about equally the labor of feeding the young throughout their period in the nest. It was quite different with D. pubescens, for in this species the female fed the young less and less as they grew older, feeding them very little or not at all during the last five days

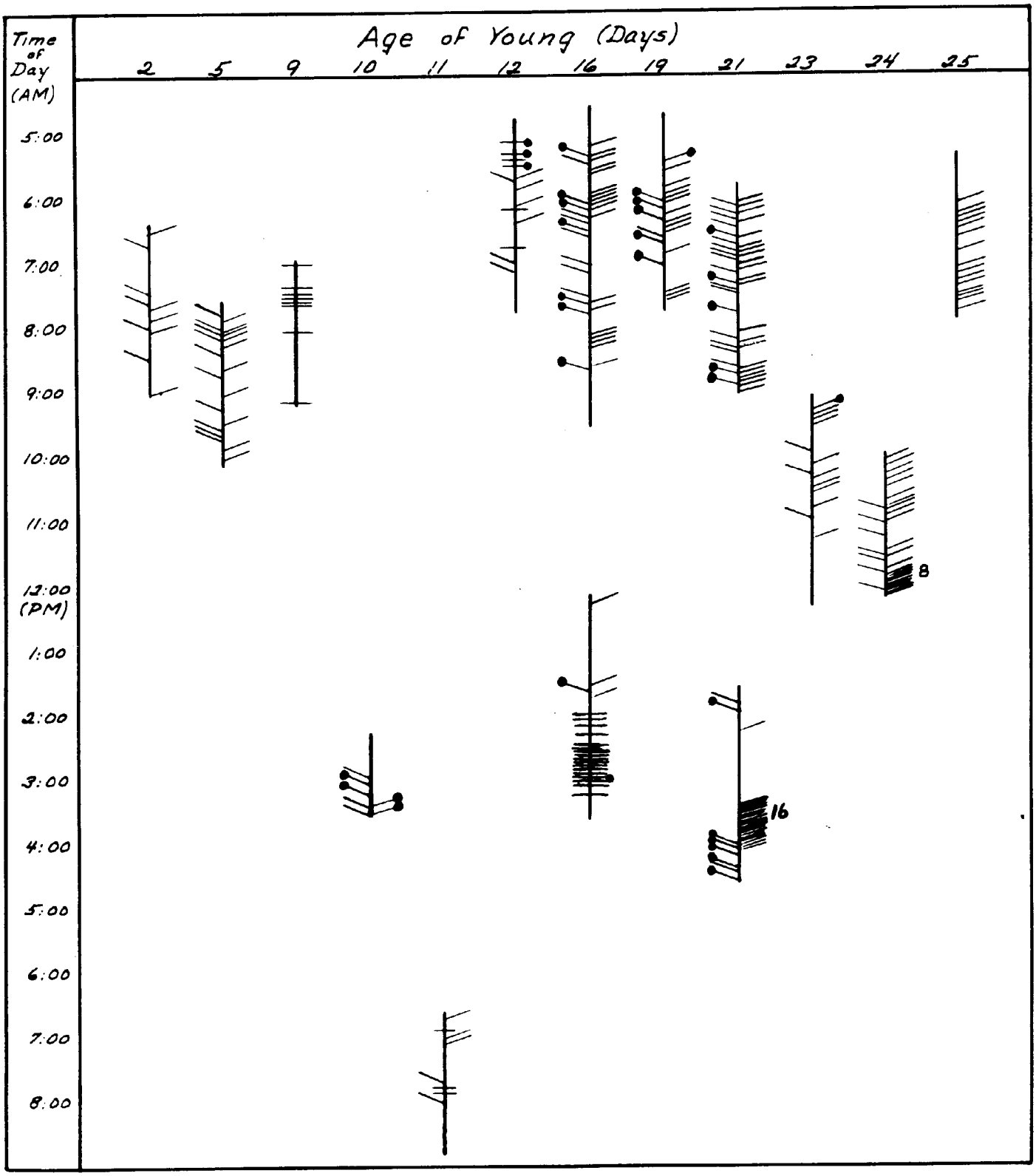
Explanation of Figure 8

Feeding of the Young and Nest Sanitation by the Hairy Woodpecker

The period of observation at each nest is indicated by the vertical lines. The visit of an adult to the nest to feed the young is indicated by a short line to the right or left of the vertical line. A short line to the left of the vertical indicates a visit by the male, to the right by the female, and a short line across the vertical indicates that the sex of the visiting bird was not determined.

The solid black dots at the end of some of the short lines indicate that the parent removed fecal material during its visit to the nest.

FIGURE 8


Time of Day (AM)
Age of Young (Days)
2
5
9
10
11
12
16
19
21
23
24
25
5:00
6:00
7:00
8:00
9:00
10:00
11:00
12:00 (PM)
1:00
2:00
3:00
4:00
5:00
6:00
7:00
8:00
8
16

they were in the nest.

The growing indifference of the females about caring for the young has been noted in D. major by Pynnonen (1939:117). At one nest he saw the female feed the young when they were 2 and 12 days old, but when the young were 19 days old the female no longer helped feed them. At another nest (1939:137) the female brought food to the young in the nest but she dropped the food or ate it herself instead of feeding it to the young. Pynnonen (1939:135) stated that the female D. minor also left most of the care of the young to the male. Pynnonen's (1939:134-135) observations at one nest of D. leucotos showed that the sexes of that species behaved like those of D. major and D. minor.

My observations were limited to three nests of D. villosus, however, at each one it was evident that the female did her share of the labor of feeding the young. Quite unlike the other four species mentioned, the female D. villosus actually increased her labors during the last few days that the young occupied the nest.

Feeding Range

Downy

The Downys gathered food for their nestlings within a radius of about 200 yards or less from the nest. The greatest distance from its nest I ever saw a parent gathering food for young was 210 yards. Quite often the parents gathered food in trees immediately adjacent to the nest tree. On one occasion a male spent nearly ten minutes digging several grubs from the nest stub at a point only a few feet below the nest entrance. The male ate the several grubs he secured and then flew to a nearby tree to gather food for the young in the nest.

Hairy

While gathering food for their nestlings the Hairys ranged from the immediate vicinity of the nest to more than 900 yards away. I frequently found the adults 200 to 400 yards from their nests and on one occasion found a marked female gathering food 920 yards from her nest. Sometimes the parents sought food in the immediate vicinity of the nest but generally several hundred feet or more away. They did not hesitate to fly across open fields into neighboring woodlots. The feeding range of Pair 3 and Pair 4 is plotted on Map 10.

Comparison

While gathering food for its young, Dendrocopos villosus ranged up to 900 yards from its nest, whereas D. pubescens was

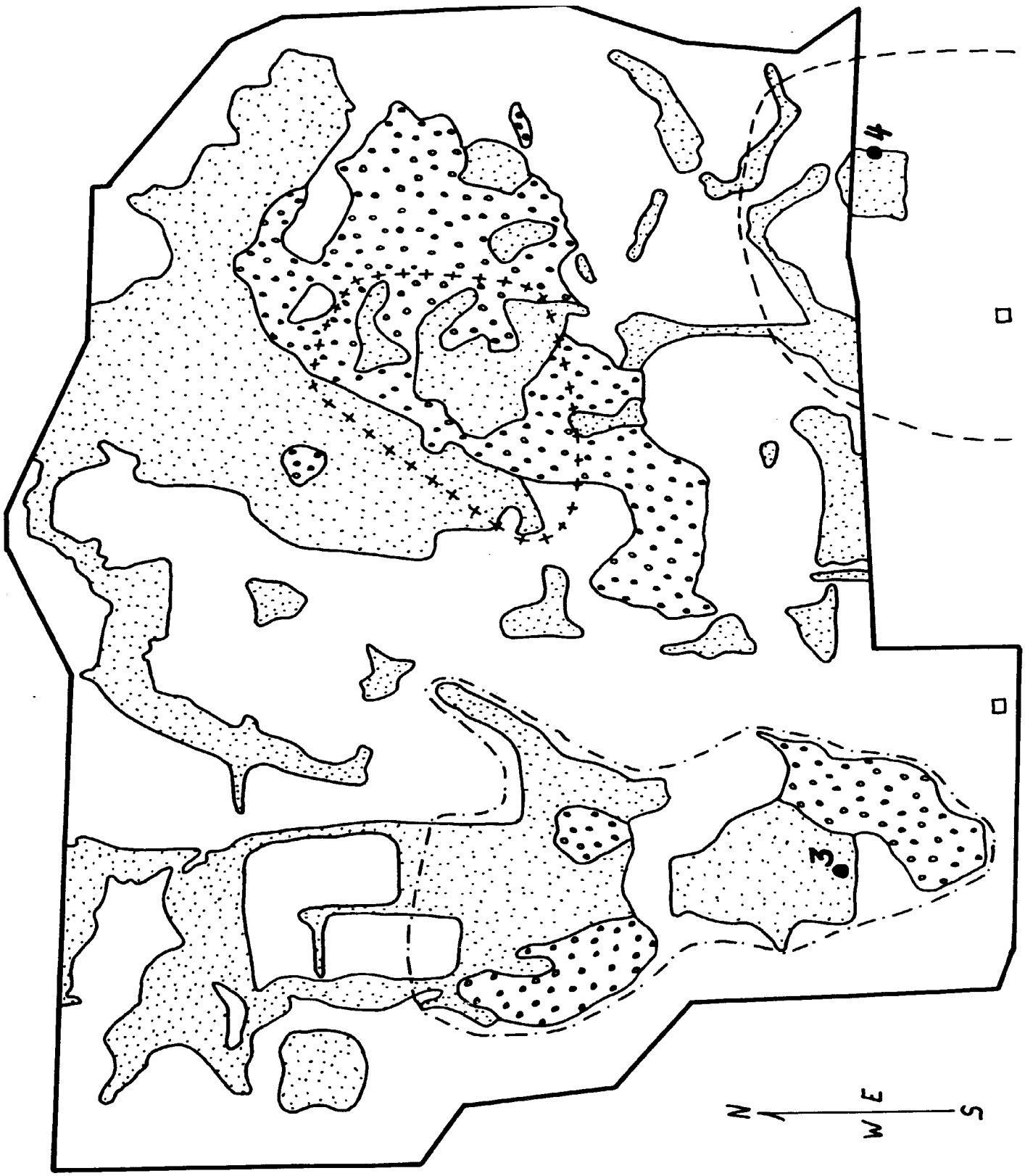
Explanation of Map 10

Foraging Range of Adult Hairy Woodpeckers While Gathering Food for Young in Nest

The foraging range of the adults of Pair 3 is outlined by the dash-dot-dash line; that of Pair 4 by the broken line, and that of Pair 5 by the line of small crosses.

The nests are indicated by large solid dots.

The oak-hickory woods are stippled and the forested swamplands are marked with open dots.



MAP 10

not seen more than 210 yards from its nest. Very little information about the feeding range of the European species during their nesting period is available to me. Durango (1945:18) stated that D. major was rarely seen more than 250 meters from its nest and generally within 50 to 200 meters.

Nest Sanitation

Downy

As shown in Figure 7, the male Downy carries out almost all of the fecal sacs. The males were seen to carry out fecal sacs 40 times, the females 3 times and an adult whose sex was not identified was seen to carry out fecal sacs once. The birds carried the fecal sacs in their bills, sometimes three or four at one time, but usually only one or two. The parents apparently disposed of the sacs at a distance from the nest as they were not seen to drop them within sight of the blind.

During the first five days following the hatching of the young, the parents presumably swallowed the fecal sacs while they were brooding the young. On one occasion a female carried out a fecal sac as she left the nest when relieved of her brooding duties by the male. The fecal sacs were apparently allowed to remain in the nest during the last day or two that the young remained in the nest.

It was very evident that the females did not carry out the fecal sacs even when there were sacs in the nest as she fed the young. On several occasions I watched the female enter the nest to feed the young and leave without carrying anything out. Immediately after her departure the male arrived, entered the nest to feed the young and then departed carrying one to several fecal sacs.

Hairy

As shown in Figure 8, the male Hairy removes most of the fecal sacs from the nest. The males were seen to carry out fecal sacs 26 times, the females 5 times. On 3 occasions the sex of the bird

carrying out the fecal sacs was not identified. The birds apparently disposed of the sacs at a distance from the nest as they were not seen to drop them within sight of the blind.

During the first 9 days after the young had hatched, the parents were not seen to carry out any fecal sacs. Presumably the parents swallowed the sacs while they were brooding the young. The fecal sacs were removed irregularly during the day, sometimes the fecal sacs were carried away on nearly every trip the male made to the nest, on other occasions no fecal material would be removed for 2 hours. The parents ceased removing the fecal sacs one to three days before the young left the nest.

Comparison

The female D. villosus carries out a greater share of the fecal sacs than does the D. pubescens female, although the males of both species carry away the much larger share. Tracy (1938:43) stated that the females of D. major and D. minor do their share of disposing of the fecal sacs, although Bussman (1946:148) found that the major male removed the fecal sacs twice as often as the female.

Comparing figures 7 and 8, it is evident that D. pubescens carried out fecal sacs more frequently than did D. villosus. The smaller species removed the fecal sacs on every fifth or sixth trip to the nest, whereas D. villosus did so on every eighth trip.

One or two days before the nestlings leave the nest, both D. pubescens and D. villosus, as well as D. major of Europe (Tracy: 1938:43) cease removing the fecal sacs from the nest. Tracy believed that the accumulation of the fecal material in the nest made it necessary for the young to leave.

Development of the Young

Downy

Young Downy Woodpeckers at hatching are blind, naked and helpless. Within 24 hours after hatching they are able to lift their heads but are unable to hold them up for more than a few seconds. When the young are between 36 and 48 hours old the parents bring them larvae for food. Tyler (Bent, 1939:57) stated "Whether in their earliest days the young birds, ... are fed by regurgitation has not been determined, but very soon after leaving the egg food is brought directly to them." I was able to see small bits of food, which looked like small larvae, in the bills of parents feeding young that were definitely less than 50 hours old.

At three days of age the young are considerably larger, nearly twice their size at hatching. I do not know when the young are able to see but at five days of age their eyes are still closed. At eight or nine days of age the young could be heard calling in the nest. They were apparently able to climb the sides of the nest to the entrance at twelve days of age for at that time the parents fed the young directly at the entrance. I was unable to make any observations on the development of the feathers after five days of age. At five days of age the feather tracts are plainly visible as dark regions on the body of the nestling although the bird is still naked.

During the last week in the nest the young kept up an almost constant calling for food. Their cries, difficult to describe, were a sort of chippering or yammering. Several days before them left the nest they uttered rattle calls and "peenk" notes very similar to those

of the adults but not as loud.

Hairy

The Hairy Woodpecker is blind, naked and helpless at birth. Young Hairys about three days old (Nest 2) responded to my tapping at the entrance by weakly holding up their heads, but lowering them in a few seconds, apparently exhausted. No feather tracts were visible on these birds at this age. When about six days old the young were still blind and the feather tracts could be made out as blackish lines or areas.

These young at Nest 2 were found dead in their nest when about eleven days old. The condition of the bodies indicated that the birds had been dead six to twelve hours. Both birds were s till blind. The feathers were still in their sheaths and projected beyong the skin several millimeters in most of the tracts. On specimen number 1 the primaries were three or more millimeters in length, the longest, number six, measured 7 mm in length. The secondaries were longer than the primaries, the ninth and tenth being 8 mm long. The feathers on the chest, abdomen and back were 4 mm or less long and those of the thighs averaged nearly 6 mm. The two median rectrices were 3 1/2 mm long and the next three on each side were 4 1/2 mm long but not as thick at their bases as the median feathers. The culmen was 15 mm and the tarsus 23 mm. The heel-pad at the proximal end of the tarso-metatarsal bone was oval shaped (7mm by 4 mm) and had about 30 tubercles.

Specimen No. 2 was somewhat smaller than number 1. The longest

primaries were numbers 4 to 7 inclusive and measured 4 mm long. Secondaries 9 and 10 were 4 1/2 mm. The feathers on the breast, back and abdomen were just protruding from the skin and some of the longest on the abdomen measured 2 and 3 mm. The median rectrices were slightly more than 1 mm in length but were noticeably heavier at the base than were the next two or three lateral feathers. These lateral rectrices were 2 1/2 mm long.

I was able to hear faintly the young in Hairy Nest 2 when those young were four or five days old. My observation blind was only about 30 feet from this nest. At Nest 3 I did not hear the young until they were about 10 days old and by the time they were 12 days old I could hear them plainly when several hundred feet away from the nest. My blind at Nest 3 was about 70 feet from the nest.

The parents were first seen to feed the young at the entrance to the nest when the young were about two weeks old (Nest 3). Apparently the nestling Hairys eyes open when they are 12 or 13 days old and soon afterwards the young start to climb up the sides of the nest cavity. The young were fed entirely from the entrance of the nest when they were about 2 1/2 weeks old.

During the last week in the nest the young called "peenk" and gave the rattle call typical of the species. Their calls were not as loud or long as those of their parents. Several times I heard the young call to the parents in the woods, the parents answering from the immediate vicinity of the nest or several hundred feet away.

Comparison

In his study of certain Finnish Woodpeckers, Pynnonen (1939: 130-131) noted that the claws on the feet increased very little in length after the young were 11 days old (Dendrocopos major and leucotus). He also noted that the wing feathers first appeared in D. major at five days of age and in D. leucotus at 9 days of age. Sherman (1910: 144) stated that the remiges and rectrices appear on young Colaptes auratus on the fifth day. D. pubescens young are still naked at five days of age, although the feathers are plainly visible under the skin and apparently about to protrude. With the young of D. villosus the feathers appear sometime after six days of age, probably the seventh or eighth day.

Pynnonen (1939:132) found that the eyes of D. major and leucotus opened on the seventh day. I did not find the eyes of D. villosus to open until the young were at least 11 days old, and Sherman (1910: 144) stated the eyes of Colaptes auratus young opened on the tenth day.

Young of D. major start calling in the nest when they are 7 days old and when 15 days of age they are able to climb to the nest entrance. D. major is very similar in this respect to D. villosus. Of unusual interest is the report by Scharnke (1930:16) who reported down on two 8 day old Centurus aurifrons santicruzi.

Reaction to Danger at the Nest

Downy

The Downys seldom showed concern when I came into the vicinity of their nests. Many times the parents continued to feed the young even when I was standing 15 to 30 feet away. At Nest 17 the parents did not stop feeding their young when a ladder was placed against the nest tree, the end of the ladder being only a few inches below the nest hole. When I was attempting to reach the young in a nest, the parents often became belligerent, swooping at my head, never actually hitting me but coming within inches of doing so.

The Downys paid almost no attention to the deer (Odocoileus virginianus) that often walked directly beneath their nests. When a deer suddenly and noisily bounded away, as was the case when they scented my presence, the Downys gave several "peenk" calls, but otherwise paid little attention.

I made only one observation on the young birds' reaction to danger. When a Crested Flycatcher (Myiarchus crinitus) looked into a Downy nest, the young in the nest became silent and remained so until several minutes after the flycatcher departed. Neither of the adult Downys was around at the time.

Hairy

The Hairys observed during this period of the breeding cycle were wary and suspicious. Often I was seen by the parents when I was 600 to 800 yards from the nest. The bird that spotted me would give a

loud rattle call or call "peenk" loudly ten to fifteen times. Sometimes it would remain in the tree from where it had first seen me or as soon as I came closer, fly away calling loudly all the time.

When I was near a nest, the action of the parents varied. At nest 1 and 3 the parents were very disturbed at my presence and called loudly. The parents at Nest 2 were very quiet whenever I was close to their nest. This nest was only six feet above the ground and the strange reaction of the parents may have been due in part to the unusual location of the nest.

Deer walking by were watched with interest by the adult Hairys but caused no alarm. However, when a deer suddenly noisily bounded away, as sometimes happened when they sensed my presence in the blind, the Hairys became excited and called "peenk" several times but became silent in a few minutes.

The presence of a Cooper's Hawk always caused considerable excitement. If the hawk was perched several hundred feet from the nest the Hairys continued feeding their young but constantly uttered excited "peenk" calls. While watching the parents bring food to the young in Nest 1 on May 14, 1941, I saw the male, who had just arrived at the nest with food, look quickly first to one side then the other and then rapidly climbed up the tree trunk six or seven feet above the nest. At this moment a Cooper's Hawk flew through the woods, passing within thirty feet of the Hairy. The Hairy kept shifting his position on the tree trunk so as to keep it between himself and the hawk. After remaining silent and motionless for two minutes, he

decended to the nest and fed the young. The young, noisy when the parent first arrived at the nest, had suddenly become silent when the male climbed up the tree and they remained so until he returned to the nest to feed them. I did not hear the parent give any warning note to the young.

The young, especially as they grew older, clammered noisily for food. Occasional calls by the parents did not cause the young to become silent; however, loud, sharp "peenk" calls or a rattle call by one of the parents instantly caused the young to become silent.

Miscellaneous Actions of the Parents while Feeding the Young

Downy

When the Downys were brooding the young the parent bringing food to the nest perched at one side of the entrance and waited for its mate to leave. When the young were no longer brooded, the parents nearly always alighted directly at the hole.

The parents frequently remained clinging to the tree at the entrance for several minutes after feeding the young. Sometimes they appeared to peck at something on the lower rim of the hole. However, I could not see any insects or other objects that the birds might have been picking up.

The Downys usually arrived flying through the woods at the same level as the nest. They always flew directly to the nest. Their departure from the nest was also direct. When carrying away fecal sacs, the birds usually flew in some other direction than the one they had been accustomed to during the last several trips. Their direction of arrival or departure was not always the same but for several to 15 trips the parent arrived and departed in the same direction.

Hairy

At Nests 1 and 3, both of which were more than 40 feet above the ground, the parents usually came flying through the woods at or close to the level of the nest. They rarely stopped at another tree but flew directly to the nest, alighting one to three feet above or below the nest hole. I saw a parent alight directly at the hole only once.

When leaving the nest the parents either flew directly from the hole or climbed one to several feet above before leaving. When carrying fecal sacs from the nest the parents always flew directly from the hole.

At Nest 2 which was only 6 feet from the ground, the parents approached the nest by flying very close to the ground. They nearly always alighted on one of the several small saplings near the nest before entering. These birds also flew close to the ground when they departed from the nest.

The Hairys did not always arrive or depart in the same direction. For example, Nest 3 was situated near the southern edge of a woodlot and the parents usually flew north from the nest and arrived from the north when coming to the nest. Occasionally one of the parents made a number of foraging trips into a wooded swamp to the south of the nest, flying across an intervening open field on each trip. Nest 1 was situated nearer the middle of a woodlot and the parents arrived at or departed from the nest in any direction.

Assocation with Other Species About the Nest

Downy

Very few other species of birds were seen near the nests of the Downys. Once a Ruby-throated Hummingbird (Archilochus colubris) flew to the entrance of Nest 17, hovered there for a few moments and then flew away.

I watched a White-breasted Nuthatch search for food in the large dead aspen in which Nest 7 was constructed. The Nuthatch had come within 10 inches of the nest when the male Downy suddenly appeared and drove the Nuthatch out of the tree. The Downy did not go into the nest but flew away and returned after several minutes with food for the young.

At Nest 17 a Crested Flycatcher boldly flew to the entrance and examined the nest, actually sticking its head into the hole. The young woodpeckers, about two weeks old, were silent when the flycatcher was at the nest. The parent Downys did not come to defend their nest and the flycatcher departed after several minutes.

Hairy

A number of other species of birds came near the nests of the Hairys and the reaction of the woodpeckers to them was generally one of indifference. A Wood Pewee (Contopus virens) started construction of its nest about 15 feet below and 20 feet to one side of Hairy Nest 3. Whenever one of the adult Hairys passed close to the Pewee nest, the Pewee flew up at the passing Hairy quite aggressively. The Hairys, however, paid very little attention to

the threats of the Pewee.

A male Baltimore Oriole (Icterus galbula) once perched within eight feet of a Hairy nest. The adult feeding the young Hairy at that time looked at the Oriole but paid no further attention to him. After the adult left, the young Hairy watched the Oriole for several minutes (June 5, 1947, Nest 3).

I observed Ruby-throated Hummingbirds near Hairy nests on at least eleven different occasions. The Hummingbird did not appear to bother the Hairys, rather they seemed to be curious about the Hairys and their nests. Sometimes the Hummingbird followed the Hairys about as the latter gathered food. Some of my observations are listed below to describe this curious behavior of the Hummingbird. Unfortunately, I was unable to determine the sex of the Hummingbird at any time.

May 22, 1947, Nest 3. A Hairy alighted in a tree about 60 feet from the nest, a Hummingbird hovered near the Hairy and then followed him as he flew to the nest. The Hummingbird hovered near the nest as the adult Hairys exchanged positions at the nest.

June 5, 1947, Nest 3. A Hummingbird followed a female Hairy into three different trees as she gathered food for her young. The Hummingbird perched 18 to 30 inches from the Hairy as she paused at various spots to dig out larvae. Later that same day a Hummingbird hovered within 8 inches of the male Hairy as he fed the young at the same nest hole.

May 18, 1941, Nest 1. A Hummingbird suddenly swooped down at the female Hairy as she was feeding her young at the nest hole. She ducked, glanced at the Hummingbird, and then finished feeding the young.

In the Huron Mountains, Marquette County, Michigan, in 1936, J. Van Tyne watched a Yellow-bellied Sapsucker come to a Hairy nest. His notes read as follows: "Sapsucker seen to visit nest June 23 at least twice (and feed young?)."

On three occasions I saw Downy Woodpeckers come close to the nests of Hairy Woodpeckers. The defense by the Downy or Hairy of their respective nesting territories against each other is discussed in Defense of Nesting Territory.

Fledging Period of the Young

Downy

At Nest 17, I secured data that indicated the interval of time from hatching to the departure of the young from the nest. On June 18, 1947, I climbed to that nest and cut into the cavity. There were 2 very small young and 2 eggs. The young were apparently hatching that day. These young left the nest on July 6 and 7, thus they were in the nest 20 days.

Hairy

Young Hairys leave the nest when 24 to 27 days old. I secured data from Hairy Nest 3 that enabled me to determine fairly closely the length of time that the young stay in the nest. The parents were not seen entering or leaving the nest on May 11 and presumably incubation was in progress at that time. On May 15 the female was seen apparently gathering food and on the morning of the following day I watched the parents enter and leave the nest in a manner that indicated they were feeding young. That afternoon I climbed to the nest but could not see its contents or hear any sounds of young. The parents were flying to and from the nest on May 17 and certainly appeared to be feeding young although no food could be seen in the bills of the parents. I estimated that the young in Nest 3 hatched about May 15.

Two of the young from Nest 3 left on June 8 and the third on June 11. The young were thus 24 to 27 days of age when they left the nest. When banding the young in this nest on June 6, I noticed

that one bird was smaller than the other two. It seems possible that the smaller bird hatched one or more days after the other two; if so incubation started before all of the eggs were laid.

Comparison

The nestling Dendrocopos pubescens which I observed remained in the nest 20 days, the young D. villosus 24 to 27 days. Pynnonen (1939:126) gave the fledging period of D. major as 21 to 22 days and of D. leucotos as 27 to 28 days. D. major, leucotos and villosus are all large species, and D. minor and pubescens are small. The season of nesting (i.e. early) of D. villosus in this country corresponds to that of D. leucotos in Europe and the nesting season of D. pubescens in this country corresponds to that of D. major and minor in Europe. The young of the early nesting species (D. villosus and leucotos) have fledging periods of 24 to 28 days; the young of the later nesting species (D. minor, major and pubescens) have fledging periods of 20 to 22 days.

Departure of the Young from the Nest

My attempts to observe the departure of young Downys or Hairys from the nest were unsuccessful. I visited Nest 17 in the morning of July 7, 1947, and found that apparently three of the four young had left the nest shortly before my arrival there or during the previous day. It seemed that only one young bird was in the nest for throughout my period of observation there, it remained constantly at the entrance of the nest and the parents did not attempt to feed any other young in the nest. Two of the other young were seen about 75 yards from the nest. The fourth bird left the nest on the afternoon of July 7.

Tyler (Bent, 1939:58) quoted an observation by DuBois who saw young Downys leave the nest. "The last two, a male and a female, left during the afternoon, each after being fed at the entrance and seeing the parent fly away. The young male flew from the nest hole straight to a tree 60 feet away. His sister quickly followed, lighting on the trunk of the same tree and following her parent up the bole in a hitching manner of their kind as though she had been practicing this vertical locomotion all her life."

Parental Care and Dispersal of Young after Leaving the Nest

Downy

I was unable to find any of the young (color-banded) Downys after they had been out of the nest more than a few days. Apparently the family groups moved to another area, for they were not seen in the immediate vicinity of the nests. In 1941 I saw several young birds and the adults together in a family group about 300 yards from their nest. Neither these young nor the parents were color-banded and I am not certain that they were the brood from the nearby nest which had left the nest about 9 days before. It seems probable that the young are able to take care of themselves within two or three weeks after leaving the nest.

It is interesting to note that of the Downys banded as young in the nest, not one was retrapped or seen on the George Reserve again. In 1941 I color-banded 11 young. In the winter of 1941-1942 I did considerable trapping but did not capture any of these young. In 1946, George M. Sutton banded 13 young Downys in nests on the Reserve. I did very extensive trapping in the following winter, 1946-1947, but did not recover any of those young birds.

One young bird that was banded as a nestling on June 8, 1941, was found dead at Bellevue, Ohio, on October 4, 1941, by Mr. Evert A. Kemp. The recovery was reported to me by the Fish and Wildlife Service and confirmed by Mr. Kemp in a letter to me. Bellevue is about 125 miles southeast of the George Reserve.

It appears that the young Downys leave their birthplace in the early fall. The data on hand indicate that all of the young Downys raised on the Reserve left that area by winter and did not return. Possibly some young do remain in the area of their birth. An immature female was banded on August 8, 1926, at Ottawa, Ontario, and recovered there six years later. An immature male was banded on August 12, 1932, at Blue Island, Illinois, and recovered at the same place six years later. These records, which were supplied to me by the Fish and Wildlife Service, indicate that these two young birds remained in the general area of their birth. Of course these birds might have moved into the area where they were captured but this does not seem likely. Young Downys are generally out of the nest by the first of July. This allows a relatively short time for the young to become independent of their parents and more into some other territory. The two young birds mentioned above were probably raised in or very near the vicinity of their capture.

Hairy

For several days after leaving the nest the young Hairys remain in its immediate vicinity. Within a week after leaving the young may disperse as far as a half mile from the nest but they still receive considerable care from the parents.

On June 9, 1947, I was unable to find the two young that had left Nest 3 on the previous day. The parents appeared to be feeding other young in addition to the one remaining in the nest. On July 3, 1947, one of the marked young females from Nest 3 was seen in a woodlot about a mile north of the nest. She was alone and appeared to be

quite successful in her search for food. Later that same day the young male from that nest was located, he was the young that had remained in the nest four days longer than the other two. He was in the nesting woods and one of the parents was nearby but I did not observe the parent feed him.

At Nest 4 the young were seen within 100 yards of the nest two days after they had left. Five days after leaving the nest one was seen in our yard, about one-fourth of a mile from the nest. Sixteen days after their departure from the nest I watched the adult male gather food in a tree in our yard and then fly with the food in his bill towards the nest woods. Two days later two hairys, they appeared to be one adult and one young, were noted along the road several hundred yards west of my house.

I do not believe that the young return to the nest after they have once left it. I arrived at Nest 3 on June 9 before the daily feeding activities had started. When feeding activities began at 6:13 only one young bird stuck his head out of the entrance to secure the food and throughout my observation period I was certain that only one young bird was in the nest. Obviously, the two young that had left this nest two days earlier had not returned to it for shelter during the night. The probable directions of dispersal of the young from Nests 3 and 4 are shown on Map 11.

Comparison

The young Dendrocopos pubescens apparently left the care of their parents about two weeks after leaving the nest. Four weeks

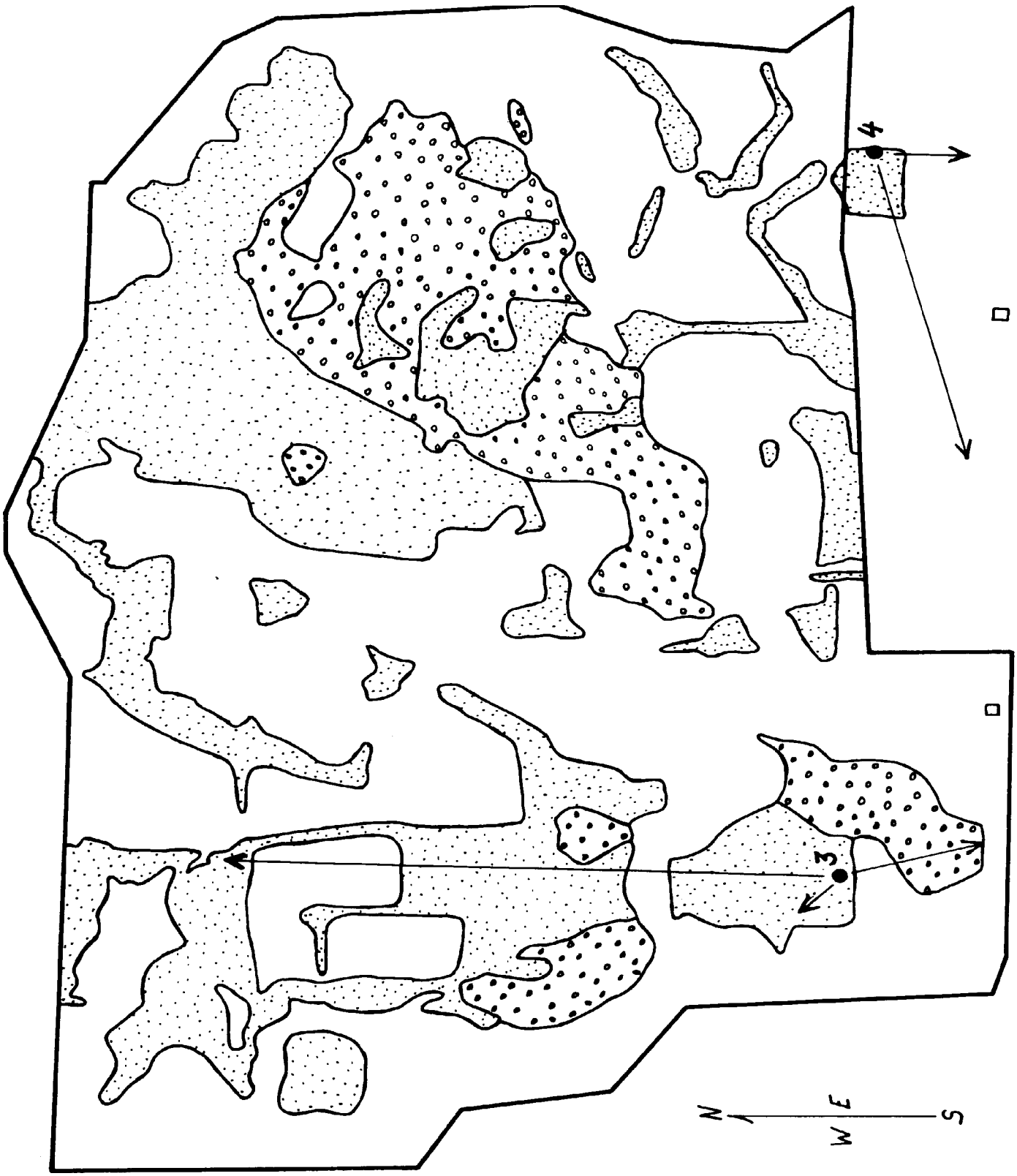
Explanation of Map 11

Dispersal of Young Hairy Woodpeckers from

Nests 3 and 4 in 1947

The nests are marked by large solid dots.

The arrows indicate points to which the young from each nest are known to have dispersed.



MAP II

after leaving the nest some of the young D. villosus were independent and others were still being cared for by the parents. Durango (1945: 18) reported that young D. major were caring for themselves soon after leaving the nest, although "...but once a ♀ was seen still feeding the brood 12 days later, and once a ♂ was found in company with 2 young after 49 days." Pynnonen (1939:139) saw a male D. major and his young in the immediate vicinity of their nest two weeks after the young had left the nest. The young of D. minor start to search for their own food as soon as they leave the nest. The parent, usually the male, feeds one young for about an hour then goes to one of the other young (Pynnonen, 1939:140). The young are thus left alone much of the time, during which they search for their own food.

Nesting Success

In 1947, Downy Nest 16 and its three small young were destroyed on June 6 by an unknown predator. This pair renested and successfully reared a brood of at least four young. On July 23, 1947, George M. Sutton saw the marked parents with the young that had apparently left the nest and noted the nest (No. 21) with one young still in it. Although their first nesting attempt was a failure, this pair is regarded as having nested successfully in 1947.

On June 13, 1942, I found a Downy nest next to the ground (Nest 11). The nest stub had fallen down, probably during a severe wind and rain storm that had occured five days earlier. The nest was originally about eight feet above the ground; after the stub had fallen the entrance to the nest was at one side and only a few inches above the gound. Three young were in the nest and one of them was dead. The nest was filthy and it was evident that the fecal material had not been removed for many days, probably not since the nest had fallen. The two living young did not seem harmed or injured in any way and seemed about ready to leave the nest. The male was seen to feed the young in this nest but the female was not seen.

In 1941, a pair of Downys was unsuccessful in its first two attempts to excavate a nest. The first hole (Nest 5) was taken over by a Red Squirrel (Tamiasciurus hudsonicus), which had enlarged the entrance considerably. The second excavation (Nest 8) was taken over by a pair of Bluebirds (Sialia sialis). In the Ann Arbor study

area a pair of Red-headed Woodpeckers took over Downy Nest 1 which probably contained eggs.

In the summer of 1946, George M. Sutton banded 13 young in three Downy nests. In one of the nests one of the five young was dead - of an undeterminable cause. Apparently all of the young banded in these three nests and the four nests in which I banded the young left successfully. From these seven nests (Nests 6, 7, 11, 12, 14, 15, 17) an average of 4.3 young were fledged. A total of 32 young were found in the 7 nests, 2 young were dead and 30 alive. Approximately 94 per cent of the young in these nests were successfully raised to the fledging stage. The above data, admittedly insufficient to be statistically significant, indicate a high degree of nesting success for the Downy Woodpecker.

My data on Hairy nests are very meager. From three nests (Nests 2, 3 and 4) a probable total of 9 young were hatched. Two young died in the nest and 7 young were successfully fledged.

Comparison

Nice (1937:143) has compiled data on the nesting success of open nesting Passerine birds. She found that 43.0 per cent of the eggs laid developed successfully into fledged young. Fifteen pairs of Song Sparrows (Melospiza melodia) raised an average of 4.3 young per pair in one season (Nice, 1937:134). In Passerine hole nesting species, (Nice, 1937:144) the nesting success averaged around 65 per cent.

Table 7

Summary of History of Downy Woodpecker Nest Studies

Nest No.	Identification of Parents	Result of Nesting
1*	none	Taken over by Red-headed Woodpeckers
2*	none	Incubation in progress
3*	none	Unknown
4	none	Construction observed
5	none	Taken over by Red Squirrel (?); second attempt Nest 8
6	Banded, marked with feathers	5 young fledged; color-banded
7	none	6 young fledged; color-banded
8	none	Taken over by Bluebirds
9	none	4 (?) young fledged
10	none	Young in Nest
11	none	Nest stub blown down; 2 young fledged, banded: 1 young dead
12	none	4 young fledged, banded; 1 young dead
13	none	Young fledged
14	♂none, ♀ "C"	6 young fledged, banded
15	none	3 young fledged, banded
16	♂ "K", ♀ "M"	6 eggs; 3 young; young destroyed (see also Nest No. 21)
17	none	4 eggs; 4 young fledged; color-banded
18	♂ "P", ♀ "U"	Young fledged
19	♂"T", ♀ "V"	Young fledged
20	♂ none, ♀ "J"	Young fledged (same tree as Nest 13)
21	♂ "K", ♀ "M"	Young fledged; was 2nd nest (1st. No. 16)

* in the Ann Arbor study area, all others were on the George Reserve.

Table 8

Summary of History of Hairy Woodpecker Nests Studied

Nest No.	Identification of Parents	History of Nest
1	none	young fledged
2*	none	2 young; deserted
3	♂ A; ♀ B	3 young; color-banded, fledged
4	none	4 (?) young, fledged
5	♂ B; ♀ none	Nest not found
6	♂ A; ♀ B	Young fledged

* in the Ann Arbor study area, all others were on the George Reserve

The data accumulated by me indicate that Dendrocopos pubescens has a nesting success of 80 per cent and D. villosus a nesting success of 82 per cent. From the data given by Pynonnen (1939:110) it is evident that D. major has a nesting success in Finland of 65 per cent.

The per cent of nesting success given by me for D. pubescens and D. villosus is probably high. However, it does seem probable that the nesting success of these two species of woodpeckers is at least equal to and probably somewhat greater than the nesting success of hole nesting Passerine birds.

Second Broods and Renesting

I found no evidence during the progress of my field studies that indicated more than one brood was raised in a nesting season by either the Downy or Hairy, although there are numerous statements in the literature that imply that these species sometimes or occasionally raise a second brood. No satisfactory report of a second brood for either species is known to me. Should some mishap occur to a nest even when the young are one week old, a new attempt is made to raise a brood and these occasional late nestings could easily be mistaken for second broods. I saw young Downys just out of the nest from about June 12 (Nest 7) to July 23 (Nest 21). Apparently the European species of Dendrocopos also have but one brood a year.

Breeding Populations in 1941 and 1947

Downy

During the 1941 breeding season, I estimated that there were 10 or possibly 12 pairs of Downys breeding on the Reserve. My estimate of breeding pairs on the Reserve in 1947 was 12 or 13 pairs, possibly as many as 15. There were two or three more breeding pairs of Downys in 1947 than in 1941.

Several pairs in 1947 nested in areas where no Downys nested in 1941 and several of the 1941 nesting territories were unoccupied in 1947. It appeared to me that 18 to 20 pairs of Downys could have nested on the Reserve yearly.

Hairy

One Hairy Woodpecker nest was found on the Reserve in 1941. One other pair of Hairys was seen on numerous occasions in the east central part of the Reserve (Big Swamp area) and twice Hairys were seen in the woodlots in the southeastern corner of the Reserve. There were at least two pairs and probably three pairs of Hairys breeding on the Reserve in 1941.

Two Hairy nests were found in 1947 (Nos. 3 and 4). A pair of Hairys were seen on several occasions in the Big Swamp area of the Reserve in 1947 and presumably they nested there. Possibly a fourth pair was present as three times that year single Hairys were seen in the extreme northwestern corner of the Reserve. Although male C and female C were color-banded on the Reserve in 1947 they are believed to have nested in one of the woodlots south of the study area. At

least three and possibly four pairs of Hairys nested on the Reserve in 1947.

The breeding population of Hairys on the Reserve is smaller than I had expected to find there. Sutton (1928:148) found 26 nests in one area of the Pymatuning Swamp in western Pennsylvania. Sutton has also done considerable field work on the George Reserve, and prior to the 1947 breeding season, he discussed with me the possible number of Hairys one would expect to find on the Reserve. On the basis of his experience with the Hairy elsewhere, he believed that there should be 8 or 9 pairs nesting there. However, from his own field observations on the Reserve he estimated that only 3 to 5 pairs nested there.

Three to 4 pairs of Hairys was apparently the number breeding on the Reserve each spring, although the area seemed suitable for a greater number. Twice during the spring of 1947 I inspected the areas to the south and east of the Reserve, about 4 sections of land, and noted probably nesting pairs of Hairys. On the basis of my experience on the Reserve and the surrounding area I estimate that there were an average of 1.5 pairs of Hairys per square mile.

Late Summer and Fall

Adult Downy and Hairy Woodpeckers were difficult to find during the late summer months. This was the time of moult for the adults and it probably contributed to their retiring habits. It was not difficult to distinguish immature birds in the field from adults. The speckled nuchal patch of the young males could occasionally be seen. More often the clean fresh plumage of the young identified them easily from the soiled and dirty adults. The young of the Downy and Hairy had the habit of spreading their tails when on a vertical branch or tree trunk, thus showing readily the white on the outer tail feathers. Adults spread their tails a little but not nearly as much as do the young. I was able to separate in the field young from adults by this method until late September or early October.

The Downy and Hairy seemed to wander about particularly in September and October. I found Hairys feeding then in isolated trees in fields, along roadsides and in other sparsely wooded areas where Hairys were rarely found at other times of the year. During this same period Downys were seen in habitats quite unfamiliar to them at other months of the year. Small trees, clumps of bushes and even weed stalks were frequented b the Downys. Goldenrod (Solidago sp.) and Mullein (Verbascum Thapsus) stalks were particularly favorite feeding places.

Food

Downy

The food of the Downy is quite varied. Beal (1911:18-22) analyzed the contents from the stomachs of 723 Downys. The specimens were collected from 33 States and Territories, the District of Columbia, and Canada, and were quite evenly distributed over the twelve months of the year. Beal found that the Downys food was 76 per cent animal and 24 per cent vegetable.

Beetles formed 21 per cent of the total diet; the wood-boring larvae alone amounting to 14 per cent. During the fall, winter, and spring months these larvae formed nearly 20 per cent of the diet, during June they formed a minimum of 4 per cent.

Scale or bark lice amounted to less than 3 per cent of the total diet. The stomachs from ten birds collected in Maine in March had a total of 93 per cent of their contents composed of scales. Caterpillars amounted to 16 per cent of the yearly diet and a large proportion of these were of wood-boring species. Ants were taken more regularly than any other food and formed 21 per cent of the diet. Grasshoppers' eggs are occasionally eaten in large numbers; 46 per cent of the total contents of the stomachs of seven birds collected in Illinois in March were grasshopper eggs.

In the vegetable class, fruits were 6 per cent of the total diet; mast composed 8 per cent. Very little cambium was found in any of the stomachs examined. The seeds of Rhus spp. (poison ivy, sumac and poison sumac) amounted to 6 per cent of the yearly diet. The foods eaten by the Downy are listed in Table 9.

Table 9

Foods eaten by the Downy and Hairy and the Per Cent of the Total Yearly Diet Represented by Each Food / 1

Foods	Downy	Hairy
	(% of diet)	(% of diet)
Grain	2	1
Fruit	6	5
Seeds	6	4
Mast	8	9
Cambium	2	2
Wood-boring beetle larvae	14	31
Weevils, etc.	3	3
Other beetles	5	9
Hymenoptera (except ants)	1	1
Ants	21	17
Hemiptera	9	2
Caterpillars	16	10
Misc. insects	3	2
Spiders, etc.	4	4

1. Data from Beal, 1911

Hairy

Beal (1911:13-17) examined the stomach contents of 382 Hairy Woodpeckers. The specimens were obtained from 33 States and Territories, the District of Columbia, and Canada, and were taken in every month of the year. He found the diet of the Hairy to be 77.7 per cent animal and 22.3 per cent vegetable. This ratio remained fairly constant throughout the year, the greatest difference being noted in June when 90 per cent of the food taken was animal and only 10 per cent vegetable.

The wood-boring larvae of beetles constituted 31 per cent of the total diet. In December these larvae made up 41 per cent of the diet and in May only 21 per cent. Other beetles formed 9 per cent of the diet.

Ants were a favorite food and represented 17 per cent of the diet. Fewer ants were eaten in summer and fall than in the winter and spring. In January, ants were eaten to the extent of 27 per cent of the total. Caterpillars formed about 10 per cent of the diet and many of them were of wood-boring species. Plant lice were found in only two stomachs and scales in only four.

In the vegetable classification fruit, mostly wild varieties, formed 5 per cent of the diet and seeds of all kinds 4.5 per cent. Cambium, mast and rubbish together constituted 11 per cent of the year's diet. The foods of the Hairy are listed in Table 9.

Feeding Habits

Downy

The Downy may be said to secure its food by two different methods, "Drilling" and "Gleaning." "Drilling" includes those foods the birds secure by excavating or drilling into wood or other substance in which the food may be.

"Gleaning" includes those foods the birds find on the surface of the bark, ground or in any other exposed situation. Foods secured by "Gleaning" are simply picked up and do not necessitate drilling to obtain.

It is possible to divide the many items of food found in Downy Woodpecker stomachs by Beal (1911:18-22) between "Drilling" and "Gleaning." Beal expressed the proportion of each food item to the nearest one one-hundredth of one per cent. I do not believe that it is possible to analyze stomach contents as accurately as his figures indicate, consequently I have rounded off to the nearest one per cent all of Beal's figures.

Grain, fruit, seeds and mast are probably all obtained by "Gleaning." Cambium (the inner bark of trees) is obviously secured by "Drilling," also one may assume that all of the "Wood-boring beetle larvae" are obtained by "Drilling." "Weevils, etc." include adult beetles that are generally found on the underside of bark or in the wood and they too are probably obtained by "Drilling." "Other beetles" are those varieties of beetles that are commonly found on the surface of bark, leaves, etc. and are presumably obtained by "Gleaning."

"Hymenoptera" other than ants, "Hemiptera," "Spiders, etc.," and "Misc. Insects" all include animals that are usually found on the surface of plants and are most likely secured by "Gleaning." "Caterpillars" and "Ants" have each been divided equally between "Drilling" and "Gleaning." Both items are secured in the winter months as well as during the warmer months. During the colder part of the year these insects were certainly dormant and were reached largely by "Drilling." The Downy obtains about 38 per cent of its food by "Drilling" and 62 per cent of its food by "Gleaning." These data are presented graphically in Figure 9.

The Downy may often be observed searching the smaller twigs and branches of trees for its food. Forbush (1907:253) noted the following observation of Mr. Baily. "On March 28, 1899, a Downy Woodpecker that he watched climbed over and inspected one hundred and eighty-one woodland trees between 9.40 a.m. and 12.15 p.m., and made twenty-six excavations for food." The observer secured one of the small twigs the bird had visited and saw that the Downy had been seeking dormant ants. A Downy may vary greatly the number of trees it visits in a period of time. For example, I watched a female Downy feed in only two trees in 30 minutes but in the next 45 minutes she visited 15 trees.

On June 4, 1947, I observed a male Downy feeding on the tip ends of the branches of red oaks. The new leaves were quite small and the bird appeared to be picking something from the base of the leaves. The food may very well have been aphids; Forbush (1907:252) stated

Explanation of Figure 9

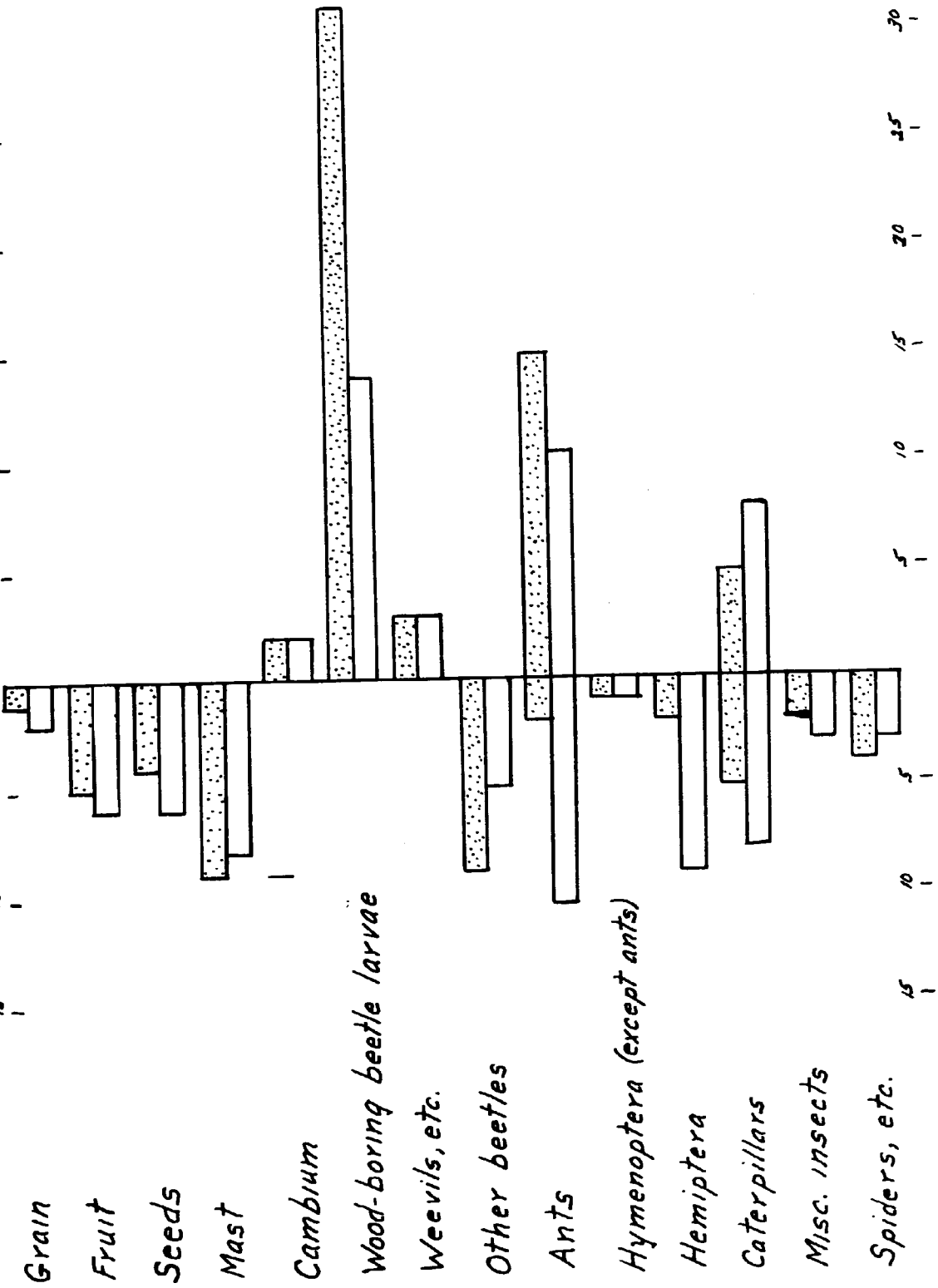
The Foods Eaten and the Method of Procurement by the Downy and Hairy Woodpeckers

The per cent of the total yearly diet each food forms is indicated by the size of the block; numbers refer to the per cent of the total yearly diet.

Blocks representing food eaten by the Hairy are stippled, those by the Downy are plain.

Blocks to the left of the vertical line indicate that the food was obtained by Gleaning, to the right by Drilling.

FIGURE 9


Gleaning
Drilling
15
10
5
1
1
5
10
15
20
25
30
Grain
Fruit
Seeds
Mast
Cambium
Wood-boring beetle larvae
Weevils, etc.
Other beetles
Ants
Hymenoptera (except ants)
Hemiptera
Caterpillars
Misc. insects
Spiders, etc.

that plant lice (aphids) "... are slaughtered in immense numbers." Downys fed in the tops of trees rather frequently and on these occasions the birds were at such heights that it was impossible to determine what they were eating or even to identify the color-band combination of those so marked.

In August and September on the George Reserve, Downys were often seen searching for food on the stalks of the mullein. They sometimes visit these plants during the winter. I saw a Downy feeding in a patch of mullein on four or five occasions during the first week of February, 1948. On March 29, 1940, a male Downy was feeding on cat-tail stalks (Typha latifolia) along the banks of the Huron River north of Ann Arbor. Examination of the stalks disclosed numerous small holes, presumably made by the bird. Standing corn stalks are another favorite of the Downy. No corn is grown on the Reserve, but I often saw Downys securing food from corn stalks in the Ann Arbor study area. Forbush (1929:270) mentioned that the Downy destroys the corn-borer.

In October and November of 1946 I was puzzled at the frequency with which Downys apparently fed on the ground on country roads. Careful observation finally disclosed that they were feeding on the meats of black walnut (Juglans nigra) and hickory (Carya ovata) nuts crushed by passing automobiles. Perhaps a major share of the mast eaten by the Downy is obtained from scraps left in the shells by squirrels. On April 4, 1940, I watched a female Downy fly to the base of a black walnut tree and peck amoung the walnut shells dropped there by the squirrels.

On one occasion a male Downy attempted to eat the pupa of a Promethea in its cocoon (April 11, 1942). The cocoon was hanging from a small branch and the Downy was unable to secure a firm foothold. The only manner in which he was able to reach the cocoon was to hang on it with his feet, but in this position he was not able to deliver very strong blows on the silken fibers of the cocoon. He finally left the cocoon after 20 minutes. I secured it and noted that the pupa inside had not been reached and little damage had been done to the cocoon itself.

When a Downy secures a particularly large larva or grub, the Downy shakes and beats the morsel of food before devouring it. On May 20, 1940, I watched a male Downy dig out from a dead branch in a medium sized oak tree a large fat grub at least an inch long. After removing the grub from the hole the Downy carried it to another tree and spent at least one minute shaking and hitting the grub against the tree trunk before finally eating it.

The Downy may be regarded as rather generalized in its feeding habits. It visits practically any type of plant stalk that will support the bird's weight -- from a giant oak to a slender cat-tail.

Hairy

The feeding habits of the Hairy may be studied in the same manner as were those of the Downy.

It will be noted in Figure 9 that the ants have been divided unequally between "Drilling" and "Gleaning." Certainly the ants eaten by the Hairy in winter were secured by "Drilling." Many more

ants were eaten in the winter than in the summer, for in January ants constituted 27 per cent of the total diet, and in mid-summer only 10 per cent. It is therefore assumed that the Hairy's preferred method of securing ants throughout the year is by "Drilling." It is quite impossible to know how many ants the Hairy secured by "Drilling" or how many by "Gleaning" during the warmer months of the year, however, I have arbitrarily divided the total amount of the yearly diet formed by ants into the two unequal parts as indicated in Figure 9.

Regarding the caterpillars, Beal does not give much information that would enable me to divide between "Drilling" and "Gleaning" with any degree of certainty. I divided equally between "Drilling" and "Gleaning" the amount of caterpillars secured by the Hairy.

The other food items in the Hairy's diet need little explanation. Cambium obviously requires "Drilling" by the birds to secure. "Weevils, etc." are adult beetles that are generally found underneath the bark. "Other beetles" include those forms of adult beetles usually found on the surface of trees and are thus secured by "Gleaning."

The Hairy secures 58 per cent of its food by "Drilling" and 46 per cent by "Gleaning." These data are presented graphically in Figure 9.

The presence of mast in the stomach contents of Hairys indicates that they must fly to the ground occasionally to secure food. Beal (1911:16) mentioned an observation of Dr. Merriam who said "that in northern New York the hairy woodpecker, like the other woodpeckers of the Adirondack region, feeds largely on beechnuts."

Beal (1911:15) also recorded Hairys feeding on the pupae of Cecropia moth cocoons "Prof. F. M. Webster states that he has seen a hairy woodpecker successfully peck a hole through the parchment-like covering of the cocoon of the Cecropia moth and devour the contents. On examining more than 20 cocoons in a grove of box elders, he found only 2 uninjured."

On August 23, 1946, I watched a female Hairy feeding two to five feet above the ground on tree trunks. She spent one-half to two minutes at each tree, then flew to another a few yards away. She started near the bottom of each tree and worked to a height of five feet, leisurely pecking here and there, then left for another tree. The Hairy finally alighted on a short stub and started pecking on the loose bark. After working on the bark for 30 seconds, she dropped to the ground and seemed to be picking up something. A few seconds later she flew back up onto the stub then dropped to the ground after spending another 30 seconds on the bark. She repeated this action eight or ten times and then left, flying out of sight. I examined the stub and found numerous beetle tunnels on the underside of the bark and assumed that the bird dropped to the ground to secure the larvae and adult beetles that had fallen there while she pecked on the bark.

J. J. Hickey (Bent, 1939:23) observed Hairys around the lower Hudson River Valley in winter scaling the bark from hemlocks in search for their insect food. In April, 1947, I noted an aspen stub where Hairys were seen working on several occasions. The bird had excavated into the rotten wood a groove that was three inches deep

at the deepest point, four inches wide at the widest point and three feet long. A pile of large chips lay on the ground at the base of the stub.

V. A. Alderson (1890:147) recorded an unusual observation. "Last summer, potato bugs covered every patch of potatoes in Marathon county, ..., Wis. One of my friends here, found his patch an exception, and therefore took pains to find the reason, and observed a Hairy Woodpecker, making frequent visits to the potato field and going from there to a large pine stub a little distance away.

"After observing this for about six weeks, he made a visit to the pine stub and found, on inspection, a large hole in its side about fifteen feet up. He took his axe and cut down the stub, split it open, and found inside, over two bushels of bugs. All had their heads off and bodies intact."

It would be interesting to know what part of its time the Hairy spends on the ground, in bushes, or in the smaller branches of trees. I have no records in my field notes that mention any instance of a Hairy in one of these situations but feel that this is partly the result of failure on my part to record this particular detail. My observations indicate that this species spends about 10 per cent of its time searching for food in places other than tree trunks or the larger branches.

In summary, it may be said that the Hairy is rather specialized in its feeding habits. The Hairy searches for its food almost exclusively on tree trunks and the larger branches. Although many of

the food items eaten by this species are also found on bushes, weed stalks, vines, etc., it rarely visits these situations in search of food.

Comparison

One of the most important requirements for a bird's existence is, of course, food. When two or more species compete for a mutually common food, that competition or rivalry may affect adversely one or all of the species involved. Before attempting to analyze the importance of the rivalry for food between the Downy and Hairy Woodpeckers I shall first describe briefly the rivalry for food among certain genera of North American woodpeckers. These genera are Picoides, Dendrocopos, Dryocopus, Sphyrapicus, Melanerpes, Colaptes, Asyndesmus, Belanosphyra and Centurus. An indication of the amount of rivalry for food that possibly occurs among these genera may be obtained by a study of the feeding habits and the food eaten by a typical species of each genus as listed in Table 10. Burt (1930) in his study of the adaptive modifications of woodpeckers, Beal (1911) in his study of the food eaten by woodpeckers, and Bent (1939) in his life history studies of woodpeckers provide a basis for this analysis.

The plant food of North American woodpeckers consists largely of mast, fruits, cambium and some seeds and grain. These foods are taken largely during those seasons of the year when each food is abundant. Because of the abundance of these foods normally, I do not believe that there is any significant amount of rivalry among woodpeckers for them. Animal food forms the greater part of the diet of most woodpeckers and it is with these foods that one may best study possible competition.

Table 10

Per Cent of the Total Yearly Diet Represented by Ants and Wood-boring Beetles Larvae in Nine Species of North American Woodpeckers /1

Genus	Ants	Wood-boring beetle larvae
Picoides sp.	7	62
Dendrocopos villosus	17	31
Sphyrapicus varius	34	
Dryocopus pileatus	39	22
Centurus carolinus	6	4
Balanosphyra formicivora	8	
Melanerpes erythrocephalus	5	
Asyndesmus lewisi	12	
Colaptes auratus	50	

/1 Data from Beal, 1911

Picoides is almost exclusively a bird of the coniferous forests (Bent, 1939) and apparently seeks its food in coniferous trees only. In this manner it differs markedly from other genera of woodpeckers that occur in the same regions. Picoides, therefore, needs no further consideration here.

Ants are eaten in various amounts by all the woodpeckers considered here. Ants may be secured by the woodpeckers from three different sources. These are: 1) underneath the surface of trees or wood, 2) on the surface of tree trunks or branches, 3) from the ground. Colaptes obtains nearly all of its ants on the ground and in this manner differs from all other woodpeckers. Thus Colaptes does not compete with any other genus of woodpecker for ants.

Centurus, Balanosphyra, Melanerpes and Asyndesmus all eat appreciable amounts of ants and they probably secure most of the ants eaten from the surface of tree trunks and branches. Asyndesmus, however, probably secures about half the ants it eats from the ground (Burt, 1930:461). The competition among these genera for ants can hardly be considered to be of much importance as ants form less than ten per cent of the total yearly diet of each.

Dryocopus, Dendrocopos and Sphyrapicus eat considerable amounts of ants but these three genera differ from the others in that they secure their ants from inside the wood. In addition, Dryocopus differs from Dendrocopos and Sphyrapicus in the places and manner in which it secures ants. Customarily, Dryocopus excavates long, deep grooves in the trunks or logs of dead trees and often digs to consider-

able depths in the wood to reach this food. Dendrocopos and Sphyrapicus secure their ants by drilling into branches and tree trunks but do not dig to the depths that Dryocopus does. Neither Dendrocopos or Sphyrapicus feed on fallen logs as Dryocopus does and Dryocopus does not search for food on the smaller tree trunks, branches and twigs as do Dendrocopos and Sphyrapicus. There probably is very little competition for ants between Dryocopus on one hand and Dendrocopos and Sphyrapicus on the other.

There apparently is some competition between Dendrocopos and Sphyrapicus for ants. Sphyrapicus is migratory and is absent from the United States and Canada during the winter. During this period it does not compete with Dendrocopos for food. In the winter range of Sphyrapicus it doubtless competes with Dendrocopos to some extent. I have observed this competition for food on the George Reserve. The Sapsucker is present there only during migration; however, during that period I frequently saw them drive away Downys from where the latter were feeding, the Sapsuckers then feeding there. There is therefore some real competition between Sphyrapicus and Dendrocopos for some foods, probably ants. This competition presumably is not harmful to either genus because it occurs only during the warmer months of the year when insect food is most abundant.

Wood-boring beetle larvae are an important component of the diet of Dryocopus and Dendrocopos. Dryocopus often scales loose bark from dead trees in its search for food and thus probably eats some food which Dendrocopos might also seek. Dryocopus confines its activities almost entirely to dead trees; Dendrocopos also searches dead trees

for food but spends more time in living trees. The several differences in the feeding habits of these two genera, some of which were pointed out in the preceding paragraph, are such that there is probably very little rivalry between them for wood-boring larvae.

Surface beetles are eaten by many of the genera of woodpeckers but usually in amounts of less than ten per cent of their respective yearly diets. Surface beetles are obtainable by the birds only during the warmer months of the year at a time when this food and most others are abundant. Because of the comparatively small amount formed by surface beetles in the diet of woodpeckers I doubt if any significant struggle for this food occurs.

In summary it may be stated that the differences in the feeding habits among the genera of North American Woodpeckers is such that there is no significant amount of rivalry or competition among them for mutually common foods.

There remains to examine the extent to which the Downy and Hairy compete with each other for food. As can be seen in Table 9, the animal diet of these birds is very similar. As pointed out before, the Downy and Hairy may secure their food by "Drilling" or by "Gleaning."

The comparative amounts of foods taken by drilling and by gleaning by the Downy and Hairy are shown in Figure 9. It is easy to assign most of the foods to one category or the other. For example, "Wood-boring beetle larvae" and "Weevils" can be secured only by "Drilling." Likewise, such foods as "Spiders," "Hemiptera" and

"Hymenoptera" are obviously taken only by "Gleaning."

"Ants and "Caterpillars" may be taken in either manner. In his examination of the stomach contents of the Hairy Woodpecker, Beal, (1911:14) found that ants formed 27 per cent of the winter diet but only 10 per cent of the summer diet. In the Downy Woodpecker (Beal, 1911:19) ants formed about 21 per cent of the diet throughout the year. Certainly the ants secured by both woodpeckers during the winter months were taken by "Drilling". Those secured in the warmer months of the year were taken by "Gleaning." I therefore divided between "Drilling" and "Gleaning" the total amount of ants secured by the Hairy (17 per cent of the total diet) to 15 per cent by "Drilling" and 2 per cent by "Gleaning." With the Downy I divided equally between "Drilling" and "Gleaning" the total yearly amount of ants taken (21 per cent). It is more difficult to separate the caterpillars so I divided them equally between "Drilling" and "Gleaning" for both species. Probably the Hairy secures most of its caterpillars by "Drilling" and the Downy most of its caterpillars by "Gleaning" but I lack data to establish this.

It can be seen in Figure 9 that the Hairy secures most of its animal food by "Drilling" whereas the Downy secures most of its animal food by "Gleaning." This difference serves to lessen the competition between them for food.

I noted that the feeding habits of the Downy and Hairy differed. The Hairy seemed to secure nearly all of its food from tree trunks and the larger branches. The Downy secured most of its food from the

smaller branches and twigs, bushes, vines, and weed stalks.

An observation I made on February 12, 1940, near Ann Arbor, partially illustrates the difference in the feeding habits of these two species. My notes read: "Male Downy feeding on saplings, seldom more than six feet above ground. He remained within a 30 foot radius for one hour. Male Hairy in same area, although feeding exclusively in large trees well above the ground. The two birds remained together for 40 minutes when the Hairy left. They made no vocal sounds."

Only once have I seen a Hairy perch cross-wise on a branch while it was searching for food. The habit of perching cross-wise on branches is common-place with the Downy. Downys may hop from twig to twig while feeding. Perching cross-wise offers no advantage to the Hairy while it is searching for food on the tree trunks or in the larger branches. On the other hand, the Downy has apparently found perching cross-wise advantageous when searching for food in the places it prefers. The Downy has little need for drilling when on the twigs, etc., and probably secures almost all of its food by gleaning in these places. Trautman also observed the difference in the feeding habits of the Downy and Hairy. Speaking of the Downy at Buckeye Lake, Ohio, he said (1940:290) "Its feeding range was seemingly much less limited than was that of the Hairy Woodpecker, for it did not confine itself to the trunks and larger limbs of large trees, but also hunted food among the smaller branches and twigs and in saplings and in the brush of thickets."

On the basis of my field observations, I believe that, while searching for animal food, the Downy spends less than one-fourth of its time in places where the Hairy would also be expected to search for its animal food. The difference in their respective feeding habits, particularly with regard to the places where each prefers to search for its food, are such that actually there is little competition between these species for food.

Economic Importance

Downy

The Downy is generally regarded as one of the most useful birds that we have. Roberts (1932:684) listed the Downy in Minnesota as "Of great value and does very little harm." Barrows (1912:348) believed that few birds were more beneficial to the farmer and fruit grower in Michigan than the Downy. Forbush (1929:270) referring to the Downy in New England said that "It would be difficult to find a bird more useful and less harmful than the Downy Woodpecker."

The Downy has been accused of drilling holes in trees to secure the sap, in fact the Downy is sometimes called the Little Sapsucker. Forbush (1929:263-269) has summarized in detail the evidence regarding the sap sucking habits of the Downy. Apparently the birds do some sap sucking but the amount is relatively small and of no economic importance.

Hairy

The Hairy Woodpecker is usually termed as beneficial to mankind. Forbush (1929:260) has pointed out that many of the insects eaten by the Hairy are of little economic consequence. He said "Certain of the wood-boring beetles taken by this bird are harmless for the most part as they work chiefly in decayed wood, but there are others that attack living trees, and the bird does not discriminate between them."

Speaking of the Hairy in Michigan, Barrows (1912:346)has said "The food of this species is similar to that of the Downy Woodpecker, but is of less account to the orchardist, since the present species

is less often found outside continuous woods... It cannot be claimed that the consumption of insects confers any great benefit upon the agriculturists, since although the percentage of beetles is very large, and many of them are boring beetles, they all are species which work only in dead wood, thus doing practically no harm."

Roberts (1932:681) has listed the Hairy in Minnesota as "Does great good in devouring insect tree-enemies,..." Roberts has probably over-estimated the economic value of the Hairy and Barrows has probably under-estimated it.

Migration

Downy

There is a difference of opinion among workers regarding the migration habits of the Downy Woodpecker. Forbush (1927:263) gave the following observation to illustrate what he believed to be migration. "As winter comes on, there is more or less migration of the Downy Woodpecker from the northern part of its range to the southward, and from higher to lower altitudes. Some ornithologists have regarded the species as non-migratory. This may be true in respect to individuals in a large part of the range of the species, but Major Mark Robinson says that early in October most individuals of the species leave his station in Algonquin National Park in the highlands of Ontario, and that before winter sets in they disappear and are seen very rarely or not at all during the winter. In the more southern and less elevated parts of Ontario the Downy Woodpecker is common throughout the winter." Taverner (1934:284-285) made no mention of migratory habits of the Downy Woodpecker in Canada.

Audubon (1834:83) claimed that "Towards winter many individuals migrate southward,...", and speaking of the species in Connecticut and Massachusetts, Bagg and Eliot (1937:338) said "There takes place to some extent a spring and fall migration, usually in late March and October, but many individual birds are fixtures in their own bailiwicks." According to Tyler (Bent, 1939:68) "Doubtless a few downy woodpeckers move southwards in autumn or early in winter, especially from the northern part of the bird's range. Dr. Charles W. Townsend in his

Ipswich notes (MS) says he sees 'evident migrants not uncommonly in October and November.'"

Ira N. Gabrielson made the following observation on the Downy Woodpecker in the Huron Mountains, Marquette County, Michigan, in October, 1936 (MS in University of Michigan Museum of Zoology). "This was the only common woodpecker. It was classed as common about Pine and Mountain Lakes on the 21st, equally abundant on the Salmon Trout River on the 22nd and on Pine Lake and Huron Mountain on the 23rd.

"Evidently there was some local shift of population during the night of the 23rd as I could not find a single specimen on the 24th in territory where they had been abundant. Only two individuals were noted at Cranberry Marsh on the 25th; several were seen at Cranberry Lake on the 26th and a single bird on the Salmon Trout on the 27th."

Bent (1939:47) listed the species (Dendrocopos pubescens) as non-migratory and added (1939:48) "While the downy woodpecker is not migratory in the accepted sense of the term, and during the months of November and December has been recorded north to Mackenzie (Fort Simpson) and central Quebec (Lake Mistassini), it appears to have some local movements and seems given to a certain amount of wandering after the close of the breeding season. In some of the more northern areas it is commoner in winter than in summer, while in the mountainous regions of the West there is apparently a vertical movement in the winter to the valley floors."

In New York State, Stoner (1932:533) and Spiker (1935:481) both regarded the Downy as a permanent resident. In Minnesota, Roberts (1932:684) listed the Northern Downy Woodpecker (D. p. nelsoni) as a winter visitant from the north. Long (1934:600) studied the status of D. p. medianus and D. p. pubescens in Kansas and concluded that "There is little migratory movement among the Downy Woodpeckers of Kansas, since specimens of the southern form have been taken both in winter and summer." He found D. p. pubescens to occur only in the southeastern corner of Kansas.

Probably more than 5,000 Downy Woodpeckers have been banded in this country and Canada but to date in the files of the Fish and Wildlife Service there has been little or no information received that indicates migration. One Downy was recovered 185 miles north of its banding place; it was banded at Elkader, Iowa, on February 2, 1925, and recovered at Balsam Lake, Wisconsin, on October 25, 1925. (See also Bent, 1939:48). The above record and all other movement records of the Downy Woodpecker on file at the Fish and Wildlife Service were supplied to me by the Service. There are two other movement records worthy of note. One bird was banded at Canton, Missouri, on January 15, 1927, and recovered 50 miles north at Burlington, Iowa, on July 5, 1927. A young Downy that I banded in the nest (Nest 6) on June 8, 1941, was found 125 miles southeast at Bellevue, Ohio, on October 4, 1941.

I observed no evidence of migration for the Downy Woodpecker. If there is a marked migration by even a small part of the population, it seems that more data than that secured to date would have accumulated from banded birds. The three movement records noted above

seem more to indicate the wandering habits of certain individuals than migration.

The habits of the Downy might easily lead an observer to believe that it migrates. The birds become very conspicuous in early spring during their courtship activites and, as they nest earlier than many observers probably realize, an apparent decrease in the numbers of Downys present results. Also in the early fall the Downy is particularly active but as winter approaches it becomes less evident.

Bent's (1939:47) statement quoted above is probably the most nearly accurate regarding the possible migratory habits of the Downy Woodpecker.

Hairy

Forbush (1927:258) believed that the Hairy migrated to some extent. He said "As winter approaches many Hairy Woodpeckers leave their forested breeding grounds and appear in orchards and villages and in parts of southeastern Massachusetts where they are almost unknown in summer. Their numbers increase considerably also in the southern parts of their range, which indicates a considerable migration. M. J. McI. Terrill of St. Lambert, Quebec, tells me that the few local breeding birds of this species disappear in early autumn and others (a very noticeable wave) appear towards the end of October or in early November.

"In early spring the movement northward and back to the forest begins, and Major Mark Robinson, a ranger in the Algonquin National Park in the highlands of Ontario, writing to me on March 11, 1920,

said that about April 1, the larger northern form of the Hairy Woodpecker left his region and that on the 10th he first noticed the smaller race which was by no means so tame as were the usual winter resident birds. He has noted a similar movement in subsequent years."

Samuels (1867:88) stated that "This Woodpecker is a rather common visitor in New England, in the spring, fall, and winter months, and is to some extent, a resident through the year. Probably the greater number retire to the North in the breeding season."

Bent (1939:21) has said "The hairy woodpecker has often been said to be a permanent resident on its breeding grounds, but this is not strictly true. The species may be present all through the year over much of its range, but there is evidence to indicate a general southward movement in fall; the individuals seen in winter are probably not the same as those seen in summer. Moreover, there is a noticeable increase in numbers in certain localities in winter."

Bent (1939:21-22) also quoted the notes of L. O. Shelley who observed the following movement of Hairy Woodpeckers in New Hampshire. "For four years I have watched, in the autumn months, passing hairies that go through, some dropping down into the valley to feed as they go along, but others passing over the valley from hill to hill (2 miles) without stopping. In passing through, they traverse in general the same route each year. They come from an eastern and continue on in a western direction at an oblique angle to the Connecticut River, which they must cross in the vicinity of Brattleboro, Vt.

"These migrants usually appear late in August or early in September and continue to arrive at irregular intervals until late in October.

It is common for one, or two, rarely more, to pass together; but such occurrences have happened, as on October 24, 1934, when, beginning soon after noon and lasting until four o'clock, the birds continued to pass through. At least 12 were seen as I walked up a roadway parallel to their course; and other moving birds were heard. It was also noticed that they kept spaced 40 to 50 yards apart, keeping abreast of one another, traversing in a leisurely manner; and as they approached a rock maple woods, the tendency was to close in like passing through the neck of a bottle and, once through the woods, again to spread out. Their progress was rather fast; and they fed little, if at all. They often called, as though to locate each other, since they were keeping about 40 yards apart, as was easily noted when they crossed pasture and mowing land.

"I followed and watched in particular a male that continued keeping along ahead of me. He repeatedly crossed the road in a zig-zag manner. Climbing to the top of a fence post or stump, he made lengthy observations, probably noting the progress of the other birds, and often answered their ringing calls. He, as well as the others, gave the appearance of a stranger in a new environment, truly a migrant."

Roberts (1932:681) listed Dendrocopos villosus villosus as a permanent resident in Minnesota and D. v. septentrionalis as a winter visitant from the north. For Michigan, Barrows (1912:346) wrote that "...certainly there is a well marked movement southward in the fall, since we have numerous reports from southern and southeastern Michigan to the effect that it is much more common in winter than in summer."

Movement records of Hairy Woodpeckers supplied to me by the Fish and Wildlife Service do not indicate any migration by this species. One bird banded at Hyas, Saskatchewan, on December 17, 1931, was recovered 48 miles west at Lintlaw, Saskatchewan, on May 13, 1939. There are three other records but the distance covered by each bird is less than 20 miles. I observed no evidence of migration of the Hairy on the George Reserve.

The apparent increase in the numbers of Hairys present in winter does not necessarily indicate migration as stated by Barrows and others. The birds wander about more and are naturally more conspicuous in the winter. The observations given by Forbush are interesting but are not corroborated by specimens. Unless more definite data are secured it seems best to regard the Hairy Woodpecker as non-migratory.

Longevity

Downy

The Fish and Wildlife Service supplied me with the age records of Downy Woodpeckers in their files. There are 31 records in which the banded bird was five years old or older. The oldest bird is a female banded at Bar Harbor, Maine, on March 31, 1932, and trapped there again on June 6, 1941. This bird was at least 10 years old when last trapped. The records include 3 birds whose known age was 8 years, 5 birds 7 years, and the others 5 or 6 years. One of my color-banded Downys was known to have been at least 5 years old when last seen. It (female C) was banded on the George Reserve on November 23, 1941; and seen there in June 1946, by G. M. Sutton, as she fed young in the nest (No. 14). I did not find this bird on the Reserve in 1947 or 1948.

From November, 1941, through February, 1942, I color-banded 17 Downy Woodpeckers on the Reserve. From December, 1946, through March 1947, I color-banded 31 Downys there. None of the 17 birds banded during the first part of the study were recaptured or seen during the second part of my study. Apparently the population of Downys on the Reserve in 1942 had been replaced with new birds by 1947. I suspect that the average life of a Downy on the Reserve to be three or four years.

Hairy

The Fish and Wildlife Service supplied me with the age records of the Hairy Woodpecker in their files. There are 15 records in which

the banded birds are 5 years old or older. An adult male was banded at Muscow, Saskatchewan, on March 20, 1927, and recaptured there on November 1, 1936. This bird was at least 10 1/2 years old when last trapped. The records include one bird 9 years old and the rest range from 5 to 7 1/2 years old.

I color-banded one Hairy (female A) in 1941 but did not find it during the last half of my field study. Male A and female B were apparently a mated pair when captured in January, 1947, and their nest (Nest 3) in 1947 probably represented at least the second year this pair had nested. I found these same birds nesting together again in 1948 (Nest 6). As the 1948 nest was presumably at least the third nesting of this pair, these birds were probably four years old or older when last seen.

Flight

Downy

The flight of the Downy is rather slow and undulating; the undulations are similar to but not as deep as those of the Goldfinch (Spinus tristis). When flying short distances, as from one nearby tree to another, the flight is generally direct and level. Just before alighting on a trunk or vertical branch, the bird often swerves sharply upwards one to several feet. Generally the flight is almost soundless but sometimes, for reasons which I could not observe, the wing beats were plainly audible.

Hairy

The flight of the Hairy is slow and undulating, quite similar to the flight of the Flicker (Colaptes auratus) but less bounding. It is characteristic for the Hairy to call "peenk" several times as it leaves it perch. The flight is direct and without undulations when short distances are traversed.

On August 5, 1941, a male Hairy suddenly flew over my head, flying very fast and making a flapping-like noise with the wings. He darted around several trees and alighted in a tree 200 feet away. The speed of the bird amazed me; there were no undulations in the flight and the wing beats were rapid and continuous.

On April 17, 1941, I watched a pair of Hairys feeding. Sometimes when one or the other bird flew to another tree it made a rather loud flapping-like noise with the wings although the flight was comparatively slow. It seemed to me at the time of the observation that the noisy flight was performed at will by the birds.

Bathing

I did not see either a Downy or Hairy bath, but on one occasion a female Downy that came to a nest had apparently just been bathing. I had discovered a nest and the male was calling loudly in a protesting manner at my presence. In a few minutes the female appeared with her feathers quite wet and disheveled. She had apparently interrupted her bathing activities to assist in the defense of the nest. She made no sounds and in a moment or two after her arrival she retired to a nearby tree and began to shake herself and smooth the feathers with her bill.

Merriman (1920:348) reported an instance of "snow bathing" by a female Downy. He stated "This morning a female Downy Woodpecker that I was watching flew to a horizontal branch and proceeded vigorously to bathe in the loose snow lying there. Like a Robin in a puddle...(the bird) ducked her head, ruffled her feathers, and fluttered her wings, throwing some of the snow over her back and scattering the rest to the winds. As all the snow fell off one part of the branch, she moved to another, until she had cleared a place about two feet long. Two forks held more snow than the straight limb, and apparently...(the) Downy enjoyed herself immensely when she came to them."

Preening

Downy

I never saw a Downy preening itself, even though every field observer commonly sees other species doing so. On five or six occasions I found Downys sitting quietly in a tree, motionless except for slight movements of the head. Even in these moments of apparent idleness on the part of the bird, no preening was observed.

Hairy

I have one record of a Hairy preening. On April 6, 1941, I noted a Hairy perched near the top of a dead tamarack several hundred feet from me. The bird was busily preening its breast feathers and the side feathers under one wing. After a few minutes it flew away, calling "peenk" loudly several times as it left.

Drinking

I made no observations of a Downy or Hairy drinking water. Shelley (1935:36) watched a male Downy drink at a brook. The bird perched on a branch just above the water and dipped his bill into the water. J. Van Tyne told me that on December 28, 1943, he watched a female Downy drink at a bird bath on the ground in his yard in Ann Arbor.

Roosting

Data from the literature indicate that the Downy makes regular use of roosting holes. Sharples (1906:101) recorded the following observation "In the early winter he drilled a hole..., and I believe used it all winter as a night refuge. During the past summer it was used occasionally by the same bird, though not with any regularity." Baird, Brewer and Ridgway (1874:512) stated that during the nesting season "The male bird will sometimes prepare a separate apartment for himself, apart from his mate." A. A. Allen (1928:418) implied that a number of roosting holes are made by each bird, stating "When cold weather sets in,...(it begins to drill) roosting holes..." Allen also mentioned that one winter a Downy roosted nightly in an old wren house. Speaking of the Downy in Michigan, Barrows (1912:349) wrote "Frequently single birds are found excavating holes in midwinter, and they resort regularly to these holes to roost throughout the year."

Sometime in January or early February, 1934, several years before starting this study, early one afternoon I flushed a Downy from a stub about four feet high. Later that same day I again flushed the Downy from the hole. During the couse of this study, I did not find any Downys in roosting holes and never found any holes that were being used for that purpose. On September 24, 1946, I watched a female Downy examine a freshly constructed hole. I visited the hole frequently during the winter but never saw a Downy there again until April 8, 1947. On this date a female Downy was again seen at the

hole. I thought that perhaps the hole was to be used for a nest but it was not.

Downys probably find shelter in roosting holes, more or less regularly during the winter. They doubtless made use of roosting holes on the Reserve; certainly there was an abundance of holes in every wooded region there. The great majority of these holes were in rotten stubs or in other situations inaccessible to me.

Hairy

I did not find the roosting holes of any Hairy Woodpeckers. George M. Sutton showed me a hole about 12 feet high in a large hickory stub at which he had seen an immature female Hairy working one day in July, 1946. I visited the hole frequently after that but never saw a Hairy there.

Forbush (1907:260) wrote "While this bird often excavates a hole for winter shelter, it sometimes sleeps exposed on a tree trunk. Mr. Bailey and I once watched one that slept for many winter nights on the north side of a tree trunk in a thick grove. It attached its claws to the bark and went to sleep in much the same position in which it ordinarily climbed the tree. It invariably went to the same tree at night, and was found in the same place at daylight each morning."

Evolution

Voous believed that villosus is older than pubescens and that pubescens apparently evolved from villosus. He stated (1947:60) "From the absence of pubescens south of the glacial forest refugia within the borders of the U. S. A., contrary to the presence of several races of villosus in the Mexican and Central American mountain forests, which represent the southernmost situated refugia of arcto-tertiary forest vegetation, one may conclude that villosus is the older form and that pubescens has split up from it by isolation in some glacial period. This hypothesis is confirmed by the great similarity that exists between the southern races of villosus and pubescens, as has been shown above."

It is quite possible that pubescens has evolved directly from villosus as postulated by Voous. It seems more likely to me that these species evolved from a common ancestor.

Voous (1947:80) recognized three groups of subspecies of villosus and two of pubescens in North America. These were the Atlantic, Pacific and southern groups. The Atlantic races of pubescens are pubescens, medianus, nelsoni and microleucus and those of villosus are audobonii, villosus, septentrionalis, terraenovae, piger, and maynardi. The Pacific races of pubescens are glacialis, gairdneri, turati and leucurus and those of villosus are sitkensis, picoideus, harrisi, orius, hyloscopus, scrippsae, monticola, leucothorectis, icastus and intermedius. There are no races of pubescens in the southern group, those of villosus are jardinii, sanctorum, parvulus,

extimus and fumeus.

Voous has pointed out that the arcto-tertiary forests of North America were reduced to three separate areas during glacial periods. These three areas were the Atlantic (Voous, 1947:94-95), the Pacific (1947:82) and the southern (1947:80; see also Fig. 16, page 79). During the glacial periods the population of pubescens became separated into two parts, one confined to the Atlantic forest area and the other to the Pacific forest area. The population of villosus became separated in a similar manner with a third part of its population being confined to the southern forest area. From the eastern area, the populations of villosus and pubescens followed the spread of the deciduous forests as the glaciers retreated. The original isolated populations of villosus and pubescens in this area evolved into the present day subspecies of the eastern or Atlantic group of each species. Similarly in the west, the populations of pubescens and villosus that were present in the Pacific forest area evolved into the present subspecies in the Pacific group of each.

As the Atlantic population of pubescens spread over eastern America after the glacial periods, that population was influenced, at least partly, in subspecific development by certain environmental factors. These same environmental factors influenced the subspecific development of the villosus population in that area. The same would be true for the post-glacial development of the western populations of villosus and pubescens. During the time from the glacial periods to the present, villosus has developed into 6 subspecies from the Atlantic

population and 10 subspecies from the Pacific population. During this same period, the pubescens population in the east and west have each developed 4 subspecies. It is apparent that the villosus populations responded more readily to environmental factors or were more easily affected in their evolutionary development by environmental factors than were the corresponding pubescens populations. One may conclude that villosus is a more plastic species than pubescens.

The plasticity of the present day villosus strongly suggests to me that the immediate ancestor of villosus was also very plastic. Part of that villosus-like population evolved into villosus while another part, geographically isolated, evolved into pubescens.

Convergent or parallel evolution and mimicry may be advanced as explanations for the similarity between villosus and pubescens. The close genetic relationship of these two species is demonstrated by their very similar color patterns and life history habits and indicates a common ancestor.

Mortality Factor

The Downy and Hairy Woodpeckers are preyed upon by the Cooper's Hawk. The reactions of the Hairy towards this hawk was described under Reaction to Danger at the Nest. On April 11, 1942, I had been watching a male Downy feed near the tops of tall oaks when he suddenly became rigid and remained perfectly motionless. For several minutes he remained in this position, then very slowly shifted his position a quarter of the way around the branch on which he was perched. Here he again remained motionless and then I caught sight of a Cooper's Hawk perched in a tree about 100 feet away. After nearly five minutes the hawk flew away and the Downy commenced feeding again. While studying the food of young Cooper's Hawks on the George Reserve, F. and F. Hamerstrom found that the Downy and Hairy each constituted about one per cent of the total number of birds eaten by the hawks.

Six young Downys were banded in Nest 7 on June 8, 1941. On June 19, 1941, the band of one of these young was found under a favorite plucking roost of a Cooper's Hawk that lived in the same woods where the Downys nested.

Shrikes (Lanius sp.) occasionally secure a Downy Woodpecker and the following record is taken from the notes of B. H. Swales. "Nov. 17, 1910. watched a shrike in action in my orchard. One took after a smaller bird that I thought was a downy woodpecker. No matter where the bird flew, or how it dodged the shrike followed each and every turning. Once they came very close to me at which I yelled and tried to drive the shrike away but without success. Back and forth they

went, and were finally lost to sight, but I imagine that the old Lanius won."

Bent (1939:21) quoted the observation of B. T. Gault who saw an English Sparrow (Passer domesticus) remove young Hairys from their nest. "The hairy woodpecker is now a very rare breeder here owing to the fact that the English sparrow appropriates almost every nest as soon as it is excavated. I once saw one of these sparrows enter the hole of one of these birds, take a newly hatched bird out in its bill, flutter for an instant over the water (the nest was in a dead willow snag standing in the overflowed Illinois River bottoms), and drop the young bird into the water to drown. It then returned into the nest and soon appeared with another newly hatched woodpecker in its bill."

Shelley (1933:204) recorded an instance where Starlings (Sturnus vulgaris) drove away a pair of Hairys from their first two nests but the Hairys succeeded in their third attempt to nest that year. Starlings were present on the George Reserve but I did not observe any conflict between them and the Hairys.

Certain mammals also prey upon woodpeckers. Stoddard (1920:96) had a Yellow-bellied Sapsucker eaten by pet Flying Squirrels (Glaucomys volans). The sapsucker had been placed alive in the cage with the squirrels and it was eaten by them the first night. Burtch (1923:340-341) watched a Red Squirrel (Tamiasciurus hudsonicus) eat a young Hairy it had apparently taken from the nest. Merriam (1884:65-66) recorded a Downy that was found in the den of a mink

(Mustela vison). It seems unlikely that the mink could have captured a live Downy but probably found the bird dead.

When banding the young in a Downy or Hairy nest, I looked for whatever parasites may have been present on the birds or in the nests but found nothing, and no parasites were found on any of the adult Downys or Hairys trapped during the winter season. Weather may occasionally cause death to the woodpeckers. Downy Nest 11 was blown over during a wind storm and one of the young in the nest was killed by the accident. Lewis (1934:147) found two nests of Dendrocopos minor in which he believed that the young had died from suffocation during a heat wave which occurred at that time. The daily temperatures in the nesting season of 1941 were much warmer than average, occasionally reaching the low 90's. During the warmest part of the day I often observed the adult Downys panting heavily at the entrance of their nests.

Species Success

Dendrocopos villosus must be regarded as a more successful species than D. pubescens if one uses as a basis for comparison the distribution and formation of subspecies of each. Presumably villosus and pubescens had equal opportunities for dispersal from the Pacific and Atlantic forest refugia as the glacial periods drew to a close. If, however, one considers the comparative sizes of the populations of each, then pubescens would be regarded as the more successful species in most parts of its range.

In certain parts of the country, pubescens is less numerous than villosus. Speaking of p. gairdneri and v. harrisi in Oregon, Jewett and Gabrielson (1940:381) said. "One of the curious anomalies of bird distribution is presented by the comparative abundance of the woodpeckers of the villosus - pubescens groups. Within the range of D. v. harrisi, the villosus group is much less abundant than its smaller relative, whereas the reverse is true of southern and eastern Oregon." In the Rocky mountains, D. p. leucurus is apparently less common than D. v. monticola (Bent, 1939:36 and 51).

I regard pubescens as the more successful species in the eastern half of North America. In the western half of the continent, villosus at present is the more successful species.

The following explanation may be advanced to account for the greater success of pubescens in the east. Man has changed the environment considerably in eastern America by the cutting of the forests. The preferred habitat of villosus is the mature deciduous forests and

it is uncommon to find villosus in sparsely wooded areas. The habitat requirements of pubescens are more easily found, for in addition to deciduous forest areas, this species is also at home in orchards, small woodlots, and other semi-wooded areas. In many cases, man has destroyed the habitat of villosus but not that of pubescens. The size of the nesting territory of pubescens is much smaller than that of villosus and the breaking up of the original forest into small units has favored pubescens but has been unfavorable to villosus. It is probable that pubescens has increased in numbers since the settlement of eastern America but villosus population has remained about the same or declined.

From Bent's (1939) descriptions of the habitats of the races of villosus and pubescens in western North America it is apparent that villosus is found in the pine forests as well as the mixed and deciduous forests. D. pubescens inhabits more the mixed and deciduous forests and tends to shun the pine forests. Although villosus was concluded to be a more plastic species than pubescens the great difference in the respective racial development of the two species in the west as compared to that in the east may also indicate that villosus is an older species in the west than pubescens.

Discussion of Differences Between Dendrocopos villosus and D. pubescens

In most of their actions villosus and pubescens were found to be very similar to each other. During the breeding cycle the details of copulation, nest construction, egg laying, and the role of the sexes in incubation and brooding were the same.

The differences exhibited between villosus and pubescens may be evaluated for survival value and the possible influence on the past and future evolution of each species. As discussed under Evolution, the pubescens ancestor probably evolved from a villosus-like ancestor by geographical isolation. Physiological isolation must be attained by a population if that population is to establish itself as a distinct species when geographical barriers no longer exist. During its period of geographical isolation from villosus, pubescens became physiologically isolated from villosus. When the two populations came into contact with each other again they remained distinct. If only physiological separation exists between two species, then one may expect to find interspecific competition. There is no interspecific competition between villosus and pubescens, for in addition to being physiologically isolated, villosus and pubescens are ecologically isolated from each other. Certain differences in their habits effect physiological separation, other differences effect ecological separation.

I found that the wintering habits and pair formation activities of villosus and pubescens were closely allied in both species. In villosus the male and female of a pair wintered together and apparently

mated for life. In pubescens, the females moved in early spring from their wintering areas into those of the males and without exception I discovered the males nesting on their wintering areas. Details about the pair formation activities of either species was not obtained, however, the data on hand indicate that the pair formation in pubescens is more complex than that in villosos. The early spring movement exhibited by the female pubescens is totally unlike any action by either sex of villosus; this difference is interpreted as a physiologically isolating factor.

The courtship display activities of villosus and pubescens were the same as far as determined. There was little chance for confusion between the species, for courtship activities occurred after pair formation was completed. Drumming as associated with courtship activities was similar in both species, although pubescens drummed more than villosus.

The difference demonstrated by villosus and pubescens in the type of nest site is perhaps one of the most important ecological isolating factors between them. I often found villosus and pubescens nests in the same woodlot. The nest of villosus was typically at some height above the ground usually in a large tree; that of pubescens was typically at a height considerably less than that of villosus and in a dead tree or stub. Perhaps of equal importance is the fact that villosus nest two or three weeks earlier than pubescens. I observed no action that could possibly be interpreted as competition between these two species for a nesting site.

Presumably the larger size and greater strength of villosus has better fitted this species to construct its nests in living trees. It may be said that pubescens does not have the physical ability to nest in sites similar to those of villosus. It must be recalled that one villosus nest was in a typical pubescens nest site, and according to the literature villosus occasionally nests in dead trees or stubs and pubescens in living trees. It is entirely plausible to presume that the geographically isolated villosus-like population which eventually evolved into pubescens, developed during the period of isolation the tendency to nest in sites typical of the pubescens of today. This difference is great enough to separate ecologically the two species with regard to nest sites and there is no interspecific competition between them. The earlier nesting of villosus may be regarded as a physiological barrier between it and pubescens.

Certain interesting differences were observed in the role of the male and female in feeding the young and in nest sanitation. In villosus the male and female shared about equally the duties of feeding the young, and nest sanitation was cared for largely by the male. In pubescens the male fed the young much more than the female and nest sanitation was cared for entirely by the male. A species in which the sexes share about equally the duties of raising the young is better equipped for survival than a species in which one sex does most of the work. The tendency for the male of pubescens to assume the greater share of the work in caring for the young may eventually prove to be a serious handicap to the survival of the species.

The extensive foraging range of villosus while seeking food for its young would seem to expose the adults unnecessarily to dangers from predators. Many times I watched villosus individuals fly across open fields between woodlots and I could not help but feel that these comparatively slow flying birds were easy prey for such natural enemies as Accipiter cooperi. I saw no need for the adults to wander over such wide territories in search of food for the young as there seemed to be an abundance of food comparatively close to the nest. I secured no evidence that any villosus fell prey to predators while young were being fed in the nest; however, it appears to me that the wide foraging range of the individuals at this time is detrimental to the species.

My data are not adequate to properly determine the nesting success of villosus or pubescens. Apparently villosus averages one less young per nest than the average number of young per pubescens nest. The number of young produced by each pair of a species is of course important in the survival of the species. The survival of the young, longevity of the adults and many other factors must be considered here as large numbers of young alone may not necessarily assure survival of the species. In so far as I was able to determine, there was no difference between villosus and pubescens in the parental care of the young after fledging or in the survival of the young. In comparison with pubescens, the somewhat smaller brood of villosus may be balanced by the greater longevity of the adults.

I have pointed out in the discussion of the Food and Feeding Habits that villosus and pubescens did not compete with each other for food. D. villosus searches for its food on the trunks and larger branches of trees, pubescens searches for its food in small trees, small branches, twigs, bushes, weed stalks, etc. The two species are ecologically separated from each other in their feeding habits.

Prior to the cutting of the original forests of eastern North America, the feeding habits of villosus were presumably well suited to that species for survival. The present environment, as typified by the George Reserve, represents a considerable decrease in the area of preferred feeding habitat for villosus. The feeding habits of pubescens are such that it can cope more successfully with the present environment than villosus.

Burt (1930) has noted several adaptive modifications in the skull and pygostyle of certain North American woodpeckers. The greatest modifications were found in those forms which were most arboreal in habits and secured most of their food from under the bark or in the wood. The diet of villosus and pubescens is very similar and therefore one would expect to find about the same degree of modification in their skulls. The two species differ in the places where they gather their food and this difference is associated with a difference in the way each species uses its tail for support while perching. I have pointed out that villosus gathered most of its food on the larger tree trunks and branches. While gathering its food, villosus perches most often in a vertical position, thus using its tail almost continually for support.

In contrast to villosus, pubescens perches in a horizontal position much of the time while it is searching for its food. While climbing about on small branches, twigs, in bushes, etc., pubescens does not use its tail for support nearly as much as villosus. Therefore one should expect to find a difference in the modification of the pygostyle between villosus and pubescens. As pointed out below, there is a difference in the modification of the pygostyles.

Burt (1930:468, Table 2) found that the tibiotarsus provided a skeletal measurement that was subject to the least amount of modification among the genera of woodpeckers he studied. From his data I have constructed Table 11. The measurements of four skull characters are expressed in per cent of the length of the tibiotarsus of each species. These skull measurements are compared with similar skull measurements of Colaptes auratus. Burt (1930) has pointed out that Colaptes sp. represents most nearly the generalized ancestral form from which the other genera of woodpeckers have evolved. In a like mannaer, I have compared in Table 11 certain characters of the pygostyle of each of the three species.

It can be seen that the skulls of villosus and pubescens are very similar; the differences between villosus and pubescens are much less than are the differences between either of them and Colaptes. The difference between villosus and pubescens in the two characters of the pygostyle is greater than is the difference between pubescens and Colaptes for these same characters. The structure of the pygostyle of pubescens indicates that pubescens uses its tail for support to a less

Table 11

Comparison of the Measurements of Certain Characters of the Skull and Pygostyle With the Length of the Tibiotarsus in Each Species

Species	Skull Characters				Pygostyle Characters	
	Length of Cranium	Width of Cranium	Width at Auditory	Width of Maxillae	Length of Pygostyle	Length of Disc
	%	%	%	%	%	%
Dendrocopos villosus	72.1	62.8	62.3	31.7	46.3	26.7
Dendrocopos pubescens	73.4	64.0	63.1	29.1	41.3	23.5
Colaptes auratus	67.6	51.3	52.9	25.6	38.2	20.0

extent than does villosus.

I regard villosus and pubescens as equally arboreal in their habits, although the pygostyle characters of pubescens seemingly indicate that this species is less arboreal than villosus. My observations on the habits of pubescens indicate that it is just as arboreal as villosus and a comparison of their diets also indicates that they are equally arboreal in their habits.

One may conclude then that the structure of the pygostyle is correlated with the feeding habits of each species.

Conclusions

The following conclusions are made regarding the habits of Dendrocopos villosus and D. pubescens in the areas in which I studied them.

D. villosus winter as mated pairs while D. pubescens winter as individual birds.

The wintering area of each pair of villosus is about 800 acres, that of each individual pubescens is about 20 acres.

D. pubescens individuals do not defend their wintering area against other pubescens individuals.

D. villosus pairs nest within the limits of their wintering area.

D. pubescens nests within the wintering area of the male, the females move from their wintering area into that of a male for nesting purposes.

Pair formation in pubescens is completed by early April.

Courtship activities follow pair formation in both species.

Male and female pubescens work at excavating the nest cavity.

The chips from the nest excavation are thrown on the ground beneath the nest in both species.

Male and female pubescens share incubation duties.

Incubation generally starts before all of the eggs are laid in both species.

The eggs are laid on consecutive days by pubescens.

The average clutch size for villosus is 4 eggs, that for

pubescens is 5.06 eggs.

The average number of young per nest of villosus is 3.3, and of pubescens is 4.04.

In both species male and female brood the young, the male stays in the nest overnight.

Temperature influences the amount of brooding performed by pubescens.

Male villosus feed the young 40 per cent of the time, the female 60 per cent of the time.

Male pubescens feed the young 67 per cent of the time, the female 33 per cent of the time.

Male villosus remove 80 per cent of the fecal sacs, the female 20 per cent; male pubescens remove all the fecal sacs.

The adult villosus range as much as 1,000 yards from the nest while searching for food for the young, the adult pubescens as much as 200 yards.

Young villosus remain in the nest 24 to 27 days, pubescens 20 days.

Neither species is migratory.

The two species are physiologically and psychologically isolated from each other in the pair formation and time of nesting behavior activities.

The two species are ecologically separated in their choice of nest site and in their feeding habits.

There is no interspecific competition between villosus and pubescens.

The close genetic relationship between villosus and pubescens is indicated by the great similarity in their habits.

The two species eat the same kinds of foods but do not compete with each other because they search for food in different places.

The evolution of villosus and pubescens has presumably been from a common villosus-like ancestor and probably by geographical isolation.

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