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Title: WOODPECKERS OF THE PACIFIC NORTHWEST: THEIR CHARACTERISTICS AND THEIR ROLE IN THE FORESTS

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This thesis is a review of the literature on the woodpeckers of Oregon and Washington especially that work relating to systematics, comparative ecology, the role of woodpeckers in forest communities, and implications to forest management.

There are two main phylogenetic lines of woodpeckers in North America: the genus *Picoides* with nine members and the Melanerpine line with ten members. Three other genera are represented by single species. These monotypic genera are *Dryocopus pileatus* and *Campophilus principalis* which have evolved large size and powerful pecking ability, and *Colaptes auratus* which is adapted to terrestrial foraging. Members of the *Picoides* are typical woodpeckers, closely adapted to arboreal life and pecking in trees for a living. The Melanerpine line has evolved in many directions and exhibits a diversity of foraging techniques including flycatching and sapsucking.

Typically, woodpeckers are forest birds. They have specialized on one aspect of the forest--decaying wood. Woodpeckers require trees with rotted heartwood for excavating nest holes. Most woodpeckers also exploit dead wood as a foraging substrate.

Most woodpeckers have a large repetoire of feeding techniques. During winter when food is scarce each species concentrates on its foraging specializations. During summer differences in foraging technique become less pronounced; almost all species take advantage of abundant insects on the surfaces of trunks, branches, twigs, and on the ground and in the air.

There is ample evidence of territoriality in woodpeckers, however pairs frequently nest in very close proximity. Woodpeckers mainly defend the nest site rather than a foraging territory. All woodpeckers can excavate a nest hole. Reproduction requires from two to three months from start of excavation until the offspring are independent. With few exceptions only one clutch is produced per year.

Woodpeckers roost in holes all year around. Most species are permanent residents although many have a tendency to become nomadic in the fall.

Probably the most significant of the roles that woodpeckers play in the forest community is the provision of nest holes for cavity nesting birds which do not excavate their own hole. Woodpeckers are the primary predators of many bark and wood boring insects; their impact is sometimes great enough to prevent insect outbreaks. Wood-decaying fungi are important to woodpeckers because fungi create the conditions required by woodpeckers for excavating.

Woodpeckers throughout the world are in an increasingly vulnerable position due to man's alterations and destruction of forest systems. Changes in structure and composition are occurring very rapidly in the forests of the Northwest due to extensive harvest and intensive timber management. An easily recognizable change in the forests is the disappearance of dead wood, both standing and fallen. Woodpeckers are closely associated with this component of the forest system, and thus are in jeopardy.

Woodpeckers of the Pacific Northwest: Their Characteristics and Their Role in the Forests

by

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WOODPECKERS OF THE PACIFIC NORTHWEST: THEIR CHARACTERISTICS AND THEIR ROLE IN THE FORESTS

I. INTRODUCTION AND METHODS

Woodpeckers are of particular significance in forest systems as predators of wood and bark boring insects and as excavators providing nest holes for cavity nesting birds which do not excavate their own hole. The biology of woodpeckers is a relevant field to resource managers because intensive timber management is severely reducing suitable habitat for woodpeckers and other cavity nesting birds which depend on them.

This thesis is the result of a literature review conducted between June 1973 and March 1974. I made an effort to review all work relating specifically to woodpeckers in Oregon and Washington. For the purposes of this study the term Northwest refers to Oregon and Washington. Recent work dealing with woodpeckers which occur in Oregon and Washington but conducted elsewhere was covered in depth. I read important papers dealing with woodpecker species not occurring in the Northwest for background and comparison. The choice of topics covered in this thesis reflects the information which is available in the literature. I attempted to incorporate both natural history and theoretical ecology in this duscussion.

II. SYSTEMATICS AND MORPHOLOGY OF WOODPECKERS

A. Classification and Phylogeny

1. Introduction

The taxonomic classification of Mayr and Short (1970) has been followed in this discussion rather than that of the A.O.U. Checklist (1957). Mayr and Short's scheme reflects more recent concepts of taxonomic and phylogenetic relationships.

Piciforme fossils have been found in deposits from the Eocene (Dickinson 1953). The ancestors of the modern picids were probably dependent upon natural cavities for nest sites (Bock and Miller 1959). The selective pressure for excavating ability in woodpeckers may have been a shortage of natural cavities. Climbing and pecking modifications, developed in connection with excavating nest holes, equipped woodpeckers to invade a new feeding habitat--the tree trunks.

2. Picoides

Following Mayr and Short (1970) the genus *Dendrocopos* is merged with *Picoides*, making all species members of the *Picoides* (Table 1). Formerly the three-toed woodpeckers were assigned to the genus *Picoides* while those with four toes made up the genus

Table 1. Taxonomic classification of the woodpeckers of the Pacific Northwest (Mayr and Short 1970).

Scientific Name	Common Name	Comment
Picoides arcticus	Black-backed three-toed woodpecker	Species group
Picoides tridactylus	Northern three-toed woodpecker	
Picoides albolarvatus	White-headed woodpecker	A.O.U. *Dendrocopos albolarvatus*
Picoides villosus	Hairy woodpecker	A.O.U. *Dendrocopos villosus*
Picoides pubescens	Downy woodpecker	A.O.U. *Dendrocopos pubescens*
Dryocopus pileatus	Pileated woodpecker	
Sphyrapicus [*varius*] *nuchalis*	Red-naped sapsucker	Species group
Sphyrapicus [*varius*] *ruber*	Red-breasted sapsucker	
Sphyrapicus thyroides	Williamson's sapsucker	
Melanerpes formicivorus	Acorn woodpecker	
Melanerpes lewis	Lewis woodpecker	A.O.U. *Asyndesmus lewis*
Colaptes auratus	Common flicker	

Dendrocopos. Delacour (1951) concluded that the number of toes was not a character of enough significance to warrant generic distinction. Short (1971a) noted that the oriental genus Dinopium contains three and four toed species that are universally considered congeneric. The merger of the two genera is supported by Burt's (1930) morphological work which revealed no important differences in the color pattern, structural features, or life habits of the two groups. Goodwin (1968) considered the three-toed woodpeckers to be closer phylogenetically to new world members of the genus Dendrocopus than the old world forms of the Picoides (in the strict sense).

The history of Picoides in North America began in the Pliocene. Asian members of this genus crossed over into North America and became geographically isolated (Short 1971a). This ancestral new world form probably had a black and white barred back, a spotted breast, and a red crown, closely resembling Picoides scalaris. Early in its history there was a split leading to a less barred line occupying eastern and central North America and Montane Mexico, and a barred line which adapted to xeric conditions of the southwest (Figure 1).

The less barred line gave rise to the three-toed woodpeckers. Evolution was rapid and involved the loss of one toe, developing a broad bill, becoming melanic and evolving the retention of a juvenile crown pattern as an adult sexual recognition factor (Short 1971a).

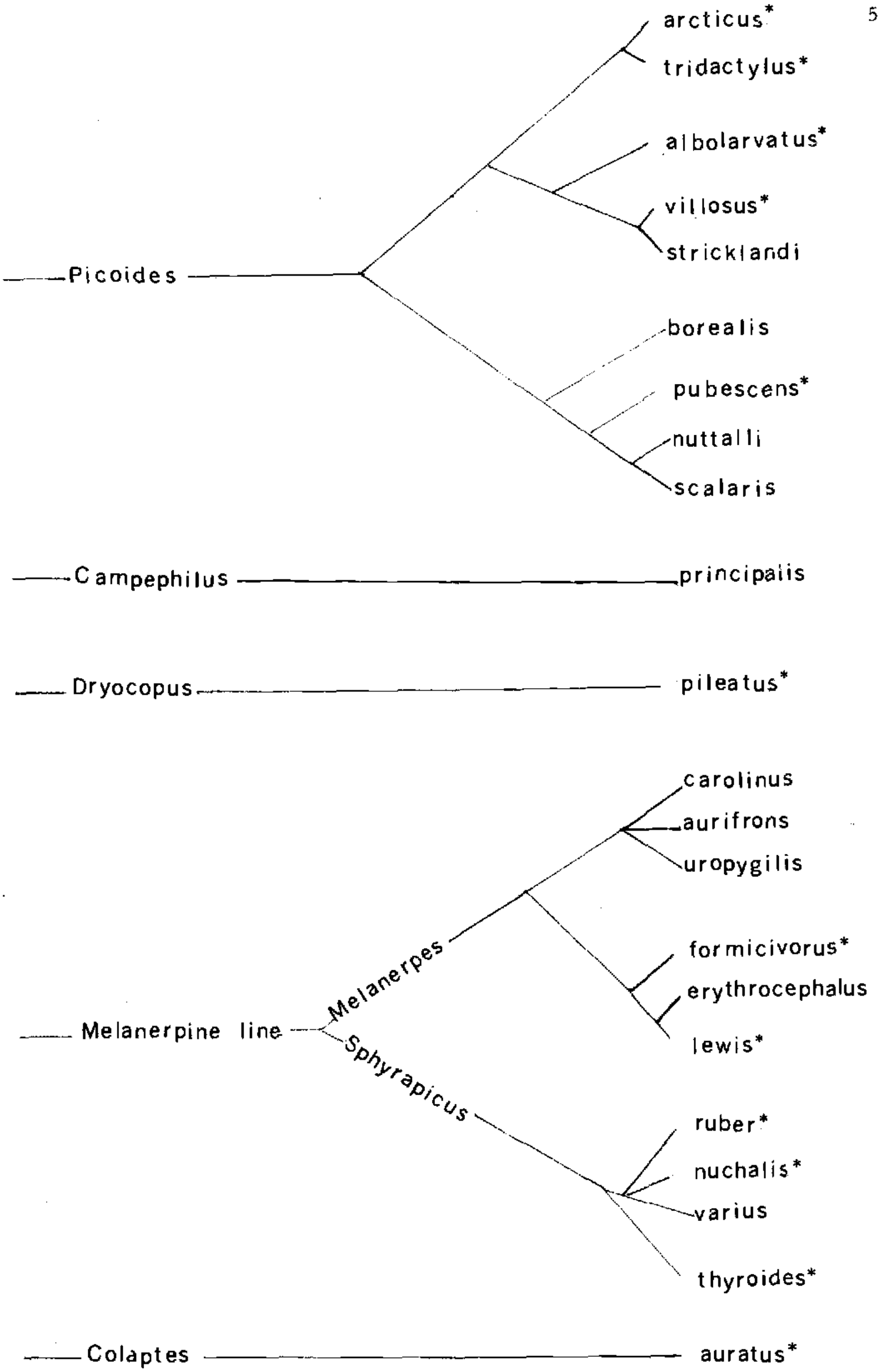

Figure 1. Phylogenetic relationships of the North American woodpeckers. Adated from Short (1971a) and Mayr and Short (1970). * Indicates species that breed in the Northwest.

These changes may have been influenced by secondary contact with scalaris and later with villosus. Short (1971a) postulated that at some later time the ancestral three-toed woodpecker entered Eurasia through a taiga forest connection across Beringia. A population isolated in the Palearctic then evolved into pre-tridactylus. Free from contact with closely related species, this species spread successfully across the Palearctic diverging from the North American pre-arcticus. Finally very recently tridactylus has reinvaded North America, to exist sympatrically with arcticus.

Picoides albolarvatus arose from the same line as the three-toeds (Short 1971a). This species evolved in the northwest and exhibited a melanic trend which paralleled that found in the three-toeds. Melanization may have evolved in response to selection against hybridization with the southwestern species stricklandi and villosus, and possibly the three-toeds and scalaris. Albolarvatus may have once been more widespread, becoming restricted in range as villosus come into sympatry with it. There are two subspecies: P. a. albolarvatus occurs in the Northwest and P. a. gravirostris is found in California.

Geographical isolation of the Mexican and North American portions of the less barred Picoides line gave rise to pre-stricklandi in Mexico and pre-villosus in the north (Short 1971a). Villosus was extremely successful, spreading throughout North America. It is ecologically the most broadly tolerant of the Picoides line. It is a strongly differentiated polytypic species which has been divided into as many as 18 races. The races found in the Northwest are orius, harrisi, and monticola.

Pubescens evolved from the barred line (Short 1971a). Smaller size was probably a feature of its evolution which may have taken place in the Northwest. It probably was very scalaris-like in appearance early in its history perhaps retaining a barred back for some time. Small size and effective reproductive isolating mechanisms apparently enabled it to become sympatric with villosus and eventually with borealis. The presence of scalaris in the southwest has prevented the expansion of pubescens to this region.

3. Melanerpine Line

The Melanerpine line, including Melanerpes (including [centurus]) and Sphyrapicus, is less specialized for excavating than the Picoides line. Many of its species feed to a considerable degree by flycatching and sapsucking and store mast for the winter.

Melanerpes formicivorus forms a species group with M. erythrocephalus, the red-headed woodpecker. Formicivorus is an uncomplicated polytypic species (Mayr and Short 1970); the Oregon race is bairdi. Melanerpes lewis is given generic distinction by the A.O.U. (Asyndesmus lewis) however Mayr and Short (1970) considered it not generically separable from Melanerpes. It is a monotypic species. Bock (1970) felt that lewis was at least as closely related to erythrocephalus as is formicivorus.

Prior to the Pliocene much of North America was covered by a transcontinental arcto-tertiary flora characterized by a mixture of deciduous and evergreen trees much as in the eastern United States today. At that time the common ancestor of lewis and erythrocephalus was probably resident in the oak woodlands of western and eastern North America. Increasing aridity and decreasing temperature during the Miocene and Pliocene caused the formation of the central plains behind the rain shadow of the Rocky Mountains; these plains isolated lewis from erythrocephalus.

In western North America, reduction of summer rainfall resulted in restriction of the mesic arcto-tertiary flora to moister upland sites, and in the loss of deciduous elements including the oaks upon which lewis depended. At the same time the sclerophyllus madro-tertiary geoflora which had arisen in southwestern North America began to spread into lowland areas of the western United States. Acorn woodpeckers which were restricted north of the tropics to the oak woodlands of the madro-tertiary geoflora, spread along with it.

As the western arcto-tertiary flora lost its oaks, the ancestral lewis woodpecker would have been forced into the xeric oak woodlands of the invading madro-tertiary flora where it would have encountered the acorn woodpecker. The competitive situation which exists today between acorn woodpeckers and lewis woodpeckers may be the result of parallel evolution in different floristic regions (Bock 1970).

The genus Sphyrapicus forms a species group composed of the species thyroides and the super species [varius]: varius (yellow-bellied sapsucker, an eastern species not occurring in the Northwest), ruber (red-breasted sapsucker), and nuchalis (red-naped sapsucker) (Mayr and Short 1970). The close relationship of thyroides and the [varius] complex is indicated by the hybridization at least twice of thyroides and nuchalis (Short and Morony 1970). Ecological separation probably acts as the reproductive isolating mechanism between these two species. In its 1957 revision of the check-list, the A.O.U. classified varius, ruber, and nuchalis as a single species although in three earlier editions they were treated as three distinct species. Short (1969) recommended full species status for the three sapsuckers. Devillers (1970) and the California Check-list (McCaskie et al. 1970) treat them as distinct species.

The ancestors of the Sphyrapicus species probably was characterized by an adult plumage resembling formicivorus. Divergence of Sphyrapicus from Melanerpes involved evolution of sapsucking habits in conjunction with related structural modifications and evolution of a distinctive head pattern (Short and Morony 1970).

4. Dryocopus and Colaptes

Dryocopus pileatus and Colaptes auratus are the single representatives of their genera in North America. The pileated has counterparts, all belonging to a group called logcocks, occupying similar niches throughout the world (Cody 1969). The flicker fills a niche occupied by the terrestrial woodpeckers throughout the world (Short 1971b). Flickers in the Northwest belong to the subspecies group cafer, red-shafted flickers.

B. Morphology

1. Introduction

The morphological adaptations of woodpeckers are related mainly to their pecking and climbing abilities. Woodpeckers possess stiff tail feathers and a large pygostyle which support the body in a vertical position on a tree trunk (Spring 1965, Scheele 1968).

The tongue is long and cylindrical and highly specialized. Proximally it is extended in two slender filaments of the hyoid bone which curl up around the back of the skull. The tongue is enclosed in a muscular sheath by means of which it is extended from the mouth. At the distal end, the tongue terminates in a hard point edged with barbs or bristles. A glandular system provides an adhesive surface to the tip of the tongue.

The skull of woodpeckers shows many adaptations for pecking. In the Picoides and Dryocopus the skull is thick and the cranium is wide. Burt (1930) described the skull of Picoides sp. as telescoped. The frontal bones are folded under as though the beak had been pushed back into the cranium. The premaxillae is wide at the base and the whole bill is generally thick. The narial openings are shifted to a lateral position and protected by a covering of feathers. The frontal bones of the Melanerpine line gradually slope to the premaxillae.

Cranial kinesis, a mechanism which permits the upper bill to move independently with respect to the brain case, is a characteristic of most birds. In woodpeckers, especially Picoides and Dryocopus, the cranial musculature is involved in a shock absorbing mechanism (Spring 1965). This change in function has resulted in a reduced angle of cranial kinesis and consequently woodpeckers have a reduced gape. The greater the ability of a woodpecker to deliver hard blows, the smaller the angle of cranial kinesis (Table 2). Greater force of blow is also correlated with an increase in the relative size of the muscles M. protractor quadrati and M. protractor pterygoidei. The force of blows with the head is distributed as tension on the interorbital septum which has become very thick. The eyes are closed during the inward movement of pecking and not opened until after impact (Spring 1965).

Table 2. Comparative morphology of 11 species of woodpeckers. Most species are sexually dimorphic; the figures listed are averages of the two sexes.

	Total Length Live (cm)	Weight (grams)	Wing Length (cm)	Length of Pygostyle (cm)	Length of Culmen (cm)	Angle of Cranial Kinesis
P. arcticus	19.2	73	12.80	1.60	3.18	17°
P. tridactylus	18.0		11.40		2.55	15°
P. albolarvatus	18.6	58		1.48	2.67	
P. villosus	18.0	70	12.95	1.52	3.03	23°
P. pubescens	13.8	24.8	9.45	1.05	1.65	
D. pileatus	36.0		23.20	2.67	5.26	14°
S. thyroides	19.8	50	13.54	1.37	2.49	
S. [*varius*]	18.6	45	12.22		2.36	23°
M. lewis	21.6		16.70	1.62	2.92	31°
M. formicivorus	19.2			1.36	2.91	21°
C. auratus	26.4	145	15.90	1.75	3.74	23°
Source	Robbins et al. (1966)	Bock and Lynch (1970)	Greenwalt (1962)	Burt (1930)	Ridgeway (1914)	Spring (1965)

Climbing ability is inversely correlated with the ability to deliver hard blows (Spring 1965). This inverse relationship occurs because maximum climbing ability requires an arrangement of muscles, tendons, and bones adapted for pulling the body inward and maintaining it close to the trunk during upward progression. Such an arrangement is poorly adapted for the delivery of hard blows which requires an outward purchase, maximum body rocking and a pronounced heel displacement before and after delivery.

2. Comparison of Species

a. Picoides.

Picoides arcticus and tridactylus are morphologically very similar. Arcticus has a solid black back and plain white outer tail feathers while tridactylus has a black and white barred back and speckled outer tail feathers.

The three-toed woodpeckers have a thick, moderately long bill, and a relatively large pygostyle (Table 2). The muscles and dimensions of these two species have evolved so that the weight of the body contributes to the momentum of the blow. The posture assumed for pecking is one in which the body is suspended at a wide angle from the trunk. The entire body is then pitched forward as the pelvis rotates about the heads of the femurs (Spring 1965).

Albolarvatus is fairly small (58 gms average weight), relative to the other Picoides (Table 2). The bill is short, 2.7 cm, and the tongue is only slightly extensile (Gabrielson and Jewett 1940).

Villosus is a heavy woodpecker (70 gms) for its size (18 cm total length) (Table 2). Relative to the other woodpeckers villosus is a generalist. It is not as well adapted to deliver hard blows as the three-toeds but it is better adapted for climbing. The stance in blow delivery is intermediate between that of arcticus and that of varius (Spring 1965). The angle of cranial kinesis is 23°, a moderate gape, but the M. protractor pterygoidei and the pygostyle are fairly large.

Pubsecens is the smallest woodpecker in North America (Table 2).

b. Dryocopus. With the exception of the probably extinct ivory-billed woodpecker, the pileated woodpecker is the largest woodpecker in North America, about 36 cm tall. The pileated's bill is 5.25 cm long, longer than its head. The point is laterally compressed forming a wedge (Conway 1957). This shape is associated with the sideways manner of pecking of pileateds. The tongue of the pileated, which may be extended up to 8.5 cm past the tip of the bill, can be bent in all directions. Mucoid saliva acts as an adhesive for catching small insects. Large insects are speared with the horny tip of the tongue. The sound of the tongue hitting a surface may be heard from 15 meters away (Hoyt 1950). The pileated is capable of delivering extremely powerful blows (Spring 1965).

c. *Sphyrapicus*. *Nuchalis* and *ruber* are similar in coloration except that *nuchalis* has a red crown and red nuchal patch separated by a plain black area, and the entire head and neck and part of the chest of *ruber* are plain red with the black and white markings of *nuchalis* only faintly visible. Plumage patterns of males and females are alike. The two species are very light, 45 grams, relative to the *Picoides* (Table 2).

Ruber and *nuchalis* are capable of delivering only weak blows. The force of the blow is delivered primarily by the neck. Prior to the delivery the abdomen is held close to the trunk surface; only the head and neck pull back before striking (Spring 1965). As predicted by Spring's theory these two species are efficient climbers but poor peckers. The individual pulls its body close to the trunk during the upward progression, keeping its tail in contact with the trunk through out the climbing motion. This inward hitching of the body decreases the component of gravity tending to pull the bird off the trunk.

Thyroides is sexually dimorphic in coloration, due to an evoluationary reversion to juvenile plumage in the female (Short and Morony 1970).

All sapsucker species have a unique tongue. Instead of a barbed tip the tongue has bristles on the end like a bottle brush, an adaptation for lapping up sap.

d. Melanerpes. The wings of lewis are proportionately larger than the wings of any other species of woodpecker (Burt 1930), and the wing load is the lightest of the woodpeckers (.20 gms/cm^2) (Bock 1970). These adaptations are associated with the flycatching behavior and migratory habits of lewis. The bill is short and thin, and has a gape far exceeding that of any other woodpecker species (Spring 1965) (Table 2). The wide gape has been acquired at the expense of the ability to deliver hard blows. Lewis has the smallest M. protractor pterygoideus muscle of the woodpeckers. It almost never pecks in wood and prefers to take over a nest hole rather than excavate its own (Bock 1970).

The morphology of formicivorus appears to be the result of compromise. Like lewis this species flycatches but it also drills holes to store acorns and excavates a nest hole in the hard wood of oaks. It has a modest gape (Table 2). The M. protractor pterygoideus muscle is only slightly smaller than that of the Picoides, and 30 percent larger than that of lewis. The bill of formicivorus is similar in length to that of villosus but slightly thinner. The pygostyle is relatively small. The wings are large; the wing load is .24 gms/cm^2.

e. Colaptes. Colaptes auratus is a terrestrial woodpecker; it follows the general trend of terrestrial woodpeckers toward dull and subdued plumage patterns (Short 1971b). In the subspecies group cafer the undersides of the wings and tail are red. The male has a red malar stripe; the female has none.

Short (1971b) postulated that arboreal woodpecker specializations preadapted the ancestor of the flicker for ground foraging. Flickers probe and dig in the ground in a manner similar to the way arboreal woodpeckers peck and scale in trees. The bill of the flicker is longer (3.7 cm), thinner, and less chisel shaped than the bill of other woodpeckers. The angle of cranial kinesis is 23° (Spring 1965), and the M. protractor pterygoideus muscle is small indicating a lack of adaptation for delivering hard blows. The tongue is very long and extensible (5 cm or more). The salivary glands which produce the sticky fluid coating the tongue are more massive in terrestrial woodpeckers than they are in arboreal species (Short 1971b). Colaptes has long legs adapted for walking on the ground, moderately short wings (Burt 1930), and a heavy wing load (.31 gms/cm^2) (Bock 1970).

III. COMPARATIVE ECOLOGY OF WOODPECKERS

A. Habitat and Distribution in the Northwest

1. Introduction

Woodpeckers typically inhabit forested areas with an abundance of dead and rotting wood, either standing or fallen. Generally woodpeckers require trees with rotted heartwood for excavating nest holes and most also exploit dead wood as a foraging substrate. Distinctions between habitats of the species can be made through differences in elevation, tree species, and canopy closure. However sympatry is common among woodpecker species, especially among those found in coniferous forests. The Northwest supports 12 of the 22 species of woodpeckers in North America. This diversity is no doubt a reflection of the vegetational and geological diversity of this region.

2. Comparison of Species

a. *Picoides arcticus* and *tridactylus*. Except for rare occurrences, the three-toeds are found only on the east side of the Cascades and in the Siskiyou Mountains (Figure 2). In subalpine regions they occur in association with engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*). At lower elevations they occur mainly in association with lodgepole pine (*Pinus contorta*)

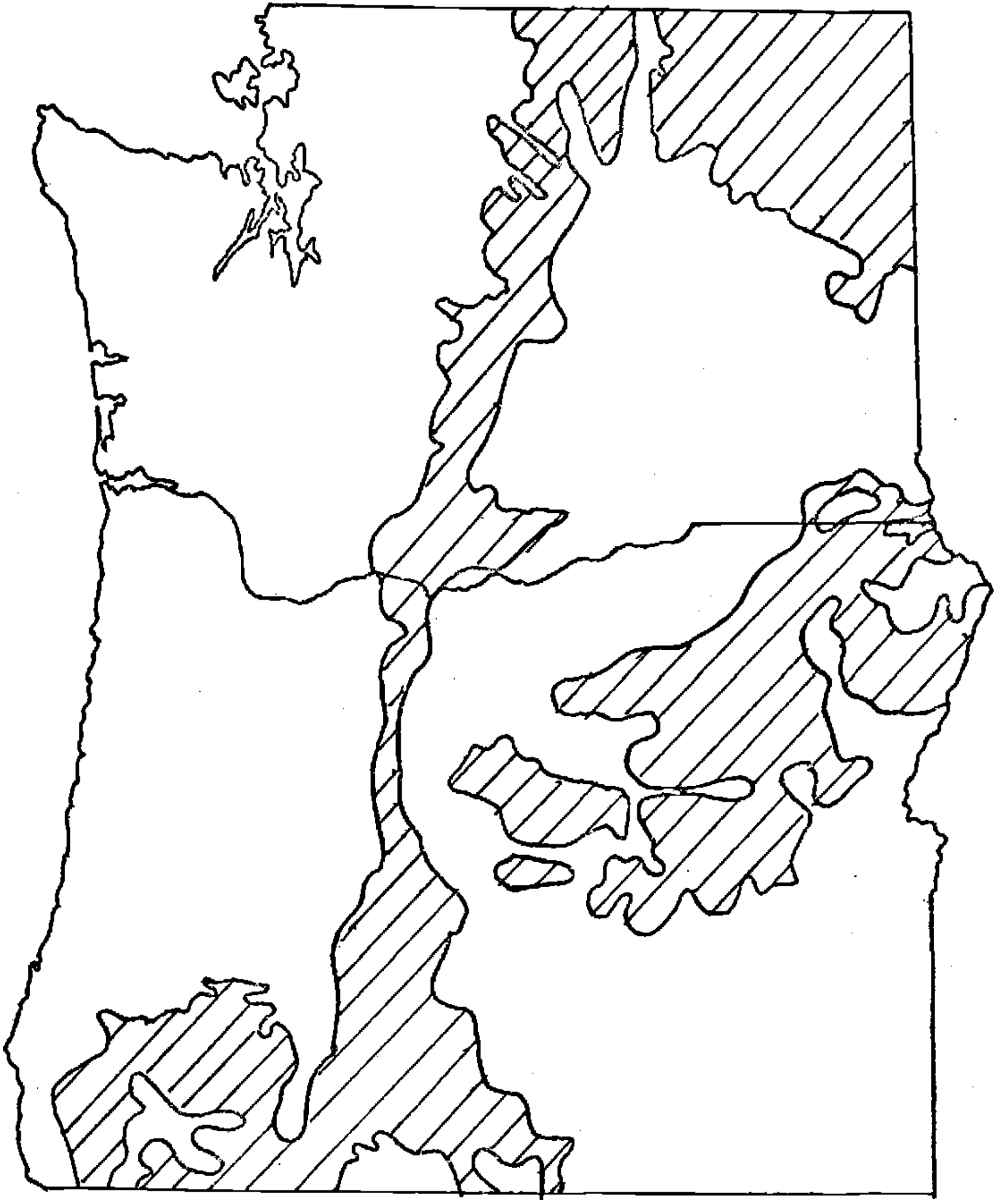

Figure 2. Distribution of Picoides arcticus and P. tridactylus.

but also with tamarack (*Larix occidentalis*), grand fir (*Abies grandis*), and occasionally with douglas fir (*Pseudostuga menziesii*) (Bent 1939, Gabrielson and Jewett 1940, McAllister and Marshall 1945, Farner 1952, Larrison and Sonnenberg 1968). Both species are attracted to areas where there are numerous dead trees as a result of fire, insect epidemic, blow down or other die-off (Whittle 1920, Bent 1939, Spring 1965, Larrison and Sonnenberg 1968, Harry Nehls, pers. comm.). It is characteristic of *arcticus* and *tridactylus* to be of extremely local and spotty distribution, probably as a product of their preference for areas containing many dead trees.

There is very little information in the literature which distinguishes these two species. They are frequently sympatric (Larry McQueen, pers. comm.), however the northern tends to occur at higher elevations than the black-backed. Weydemeyer (1928) considers *arcticus* about three times as abundant as *tridactylus* in the transition zone and *tridactylus* more common in the Canadian zone. The black-backed but not the northern is sometimes found in ponderosa pine (*Pinus ponderosa*) (Harry Nehls, pers. comm.). Robbins et al. (1966) show a more extensive distribution for the northern three-toed. They show *arcticus* as being restricted to a strip along the Cascades while *tridactylus* ranges across eastern Washington and Oregon. Gabrielson and Jewett (1940:387) state that the black-backed is uncommon in the Blue and Siskiyou Mountains being found mostly in the east Cascades and central Oregon:

> The great lodgepole pine forests lying between Bend and Klamath Falls in a more or less unbroken body from the summit of the Cascades to the eastern spurs of the Paulina Mountains is the center of (*arcticus*') abundance.

Similarly, Larry McQuees (pers. comm.) states that the black-backed is most common (never actually common) in the lodgepole belt of the Cascade area.

b. *Picoides albolarvatus*. In Oregon and Washington the white-headed woodpecker is closely associated with ponderosa pine (Bent 1939, Gabrielson and Jewett 1940, Larrison and Sonnenberg 1968, Burleigh 1972).(Figure 3). In California, the southern part of its range, the white-headed woodpecker prefers to forage on coulter pine (*Pinus coulteri*) and sugar pine (*Pinus lambertiana*) (Koch et al. 1970). Sugar pine occurs in southern Oregon and is probably utilized there by *albolarvatus* but otherwise in the Northwest this species is dependent upon ponderosa pine. Ligon (1973) found that in Idaho ponderosa pine was the only plant species importantly used by *albolarvatus*. Larry McQueen (pers. comm.) suspects that white-headed woodpeckers require large tracts of mature ponderosa pine such as are found in the Cascade lakes area.

c. *Picoides villosus*. The hairy woodpecker is not closely associated with any tree species or species group. It is usually found in forests containing some element of coniferous trees and in open

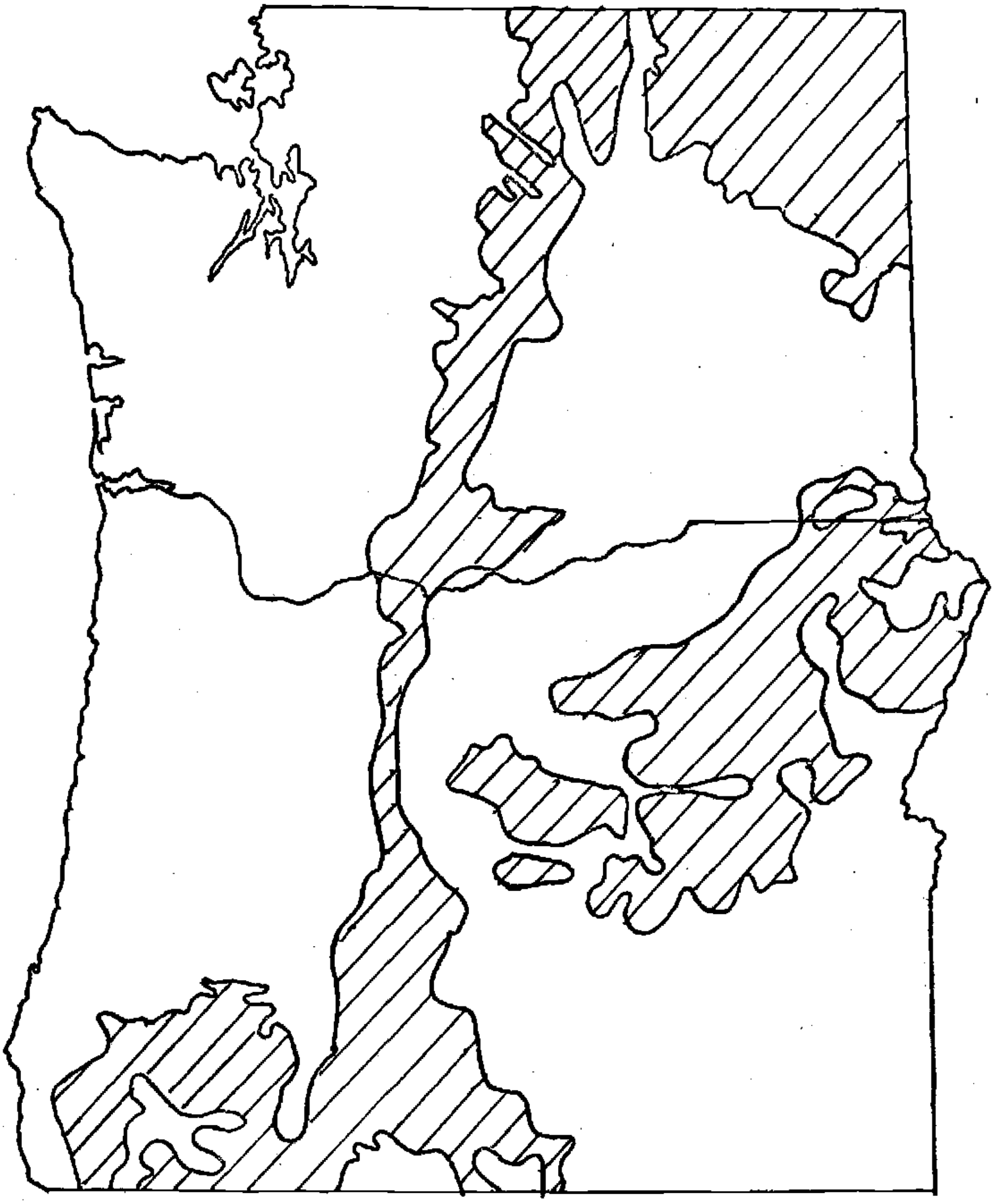

Figure 3. Distribution of Picoides albolarvatus.

rather than dense timber (Larrison and Sonnenberg 1968). This species is often found in abundance in burns and stands of dead trees (Koplin 1967), and is generally most common at low elevations although it occurs into the subalpine zone. It breeds throughout Oregon and Washington (Figure 4).

d. Picoides pubescens. The downy woodpecker is mainly a bird of deciduous woods particularly willows (Salix sp.) and alders (Alnus sp.) along streams and groves of aspen (Populus tremuloides) and cottonwood (Populus trichocarpa). It is commonly found in orchards and wooded residential areas. East of the Cascades it is rare, being found primarily along rivers. It is most abundant along the Columbia and Willamette Rivers (Gabrielson and Jewett 1940) (Figure 4). Downys may be found in coniferous forests in areas of high insect abundance resulting from burns or epidemics but they return to deciduous trees to nest (Koplin 1967).

e. Dryocopus pileatus. The pileated is an uncommon species (Bertrand and Scott 1971) found in forested regions throughout the state; it is generally most abundant in densely timbered stands of mature age (Figure 5). It usually occurs at low to moderate elevations (Gabrielson and Jewett 1940). This species is sometimes found nesting in large cottonwood stands along rivers. Bendire (1892:105) writes

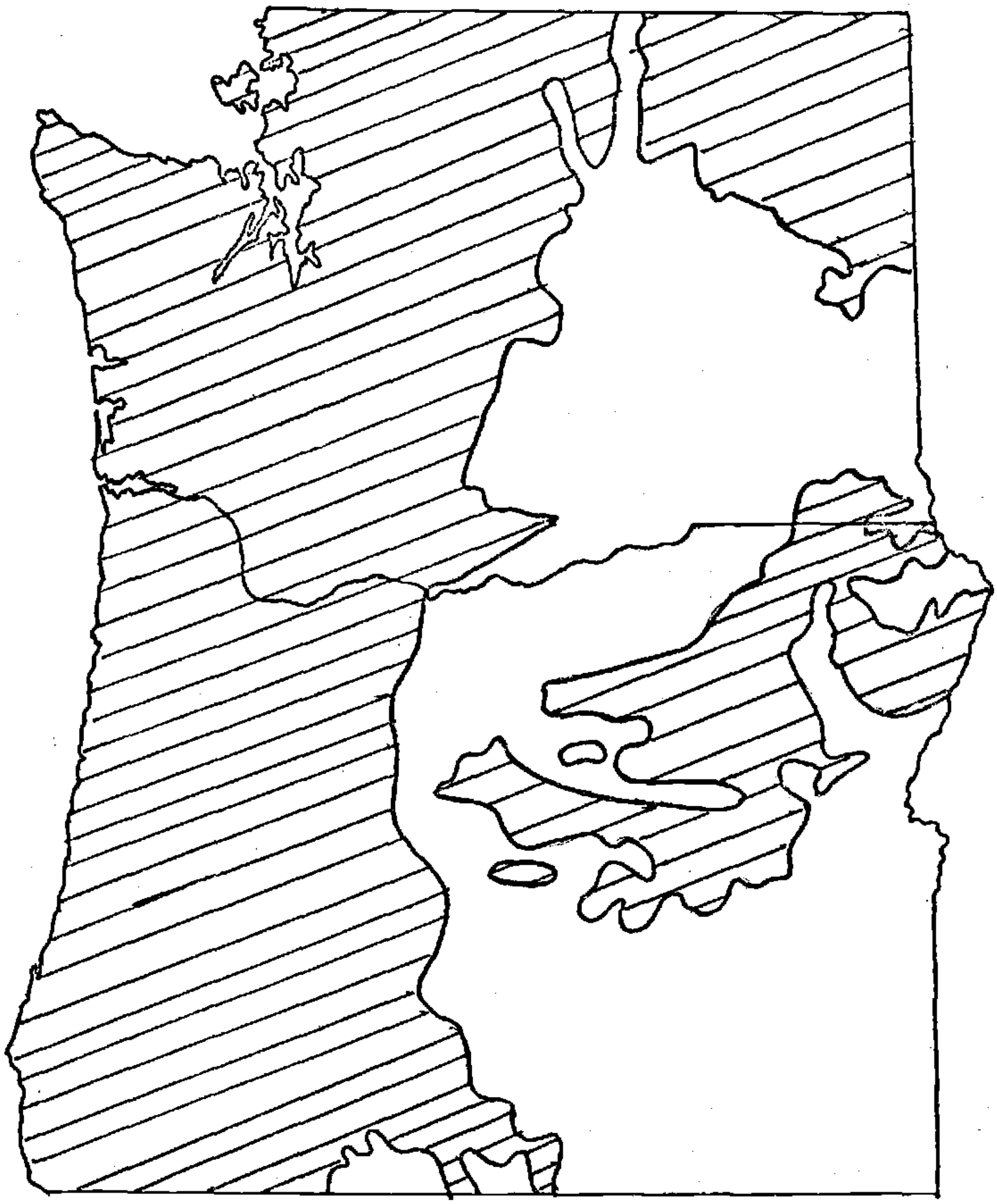

Figure 4. Distribution of Picoides pubescens and P. villosus. Pubescens is found especially in riparian habitat some of which is not indicated by this map.

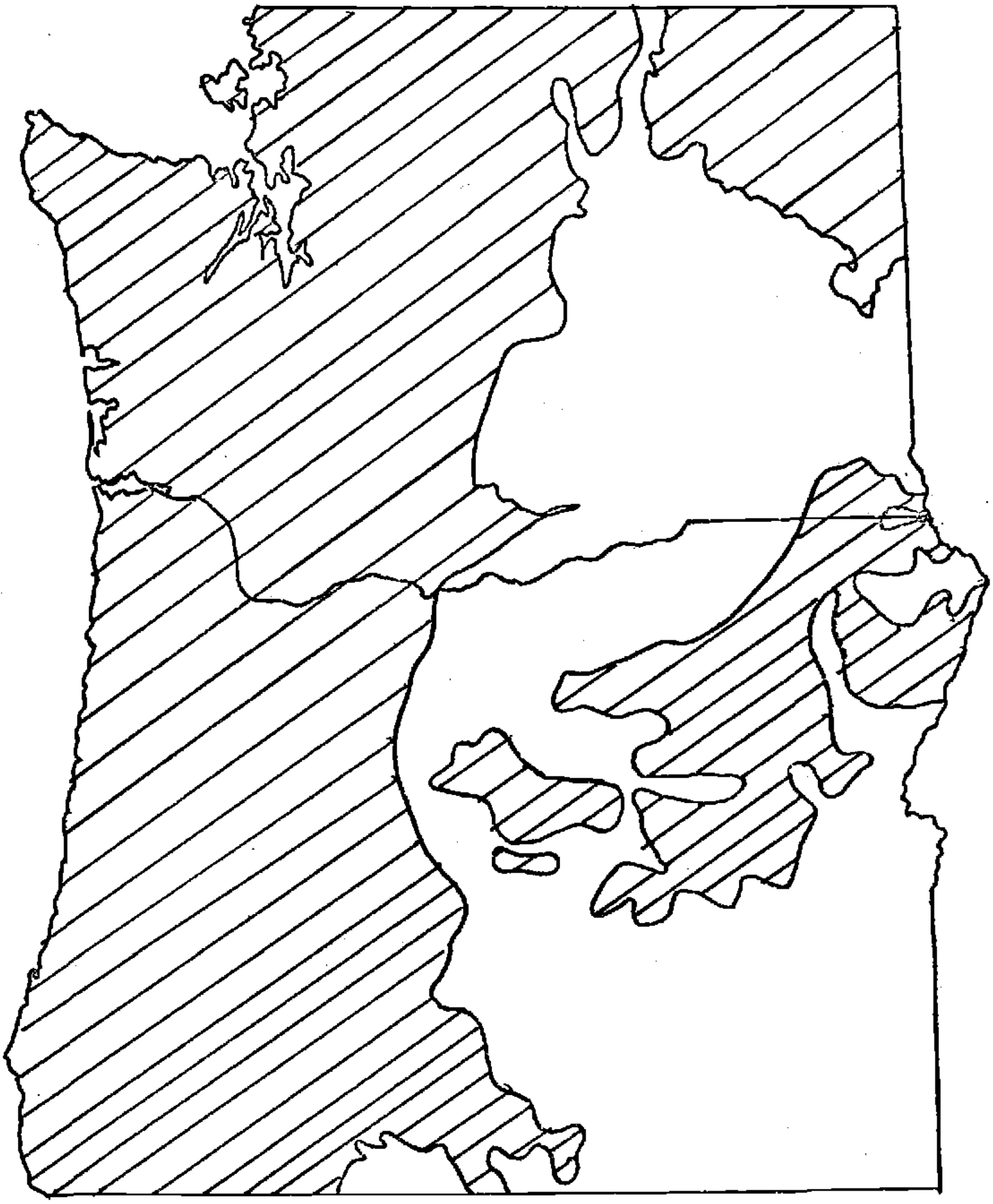

Figure 5. Distribution of Dryocopus pileatus.

> . . . the pileated is most frequently met with in the extensive burnt tracts, the so-called deadenings, where forest fires have swept through miles of fine timber and killed everything in its path.

Farner (1952) reported that at Crater Lake pileated woodpeckers have been noted in a variety of forest types but occur most commonly in lodgepole pine, white fir (Abies concolor), shasta fir (Abies shastensis), and mountain hemlock (Tsuga mertensiana).

f. Sphyrapicus thyroides. Williamson's sapsucker is an uncommon species occurring east of the Cascades (Bertrand and Scott 1971) (Figure 6). It is migratory, but winters sparingly at low elevation (Kitchin 1935). Thyroides is found principally in the Canadian zone ranging into the hudsonian above and the transition below (Jewett et al. 1953). Its habitat is dry, open coniferous woodlands, especially ponderosa pine but also in douglas fir, larch, and lodgepole pine forests. Although thyroides uses other tree species it seems to require some ponderosa pine in its habitat (Larry McQueen, pers. comm.). It may be found in small isolated pockets of ponderosa pine amidst lodgepole pine but occurs only accidentally in pure stands of lodgepole.

In Washington, thyroides is rare at higher elevations east of the crest of the Cascades and in the Blue Mountains. In Oregon it is found on the summit and eastern slopes of the Cascades, in the Siskiyous, the Blue Mountains and isolated ranges where ponderosa

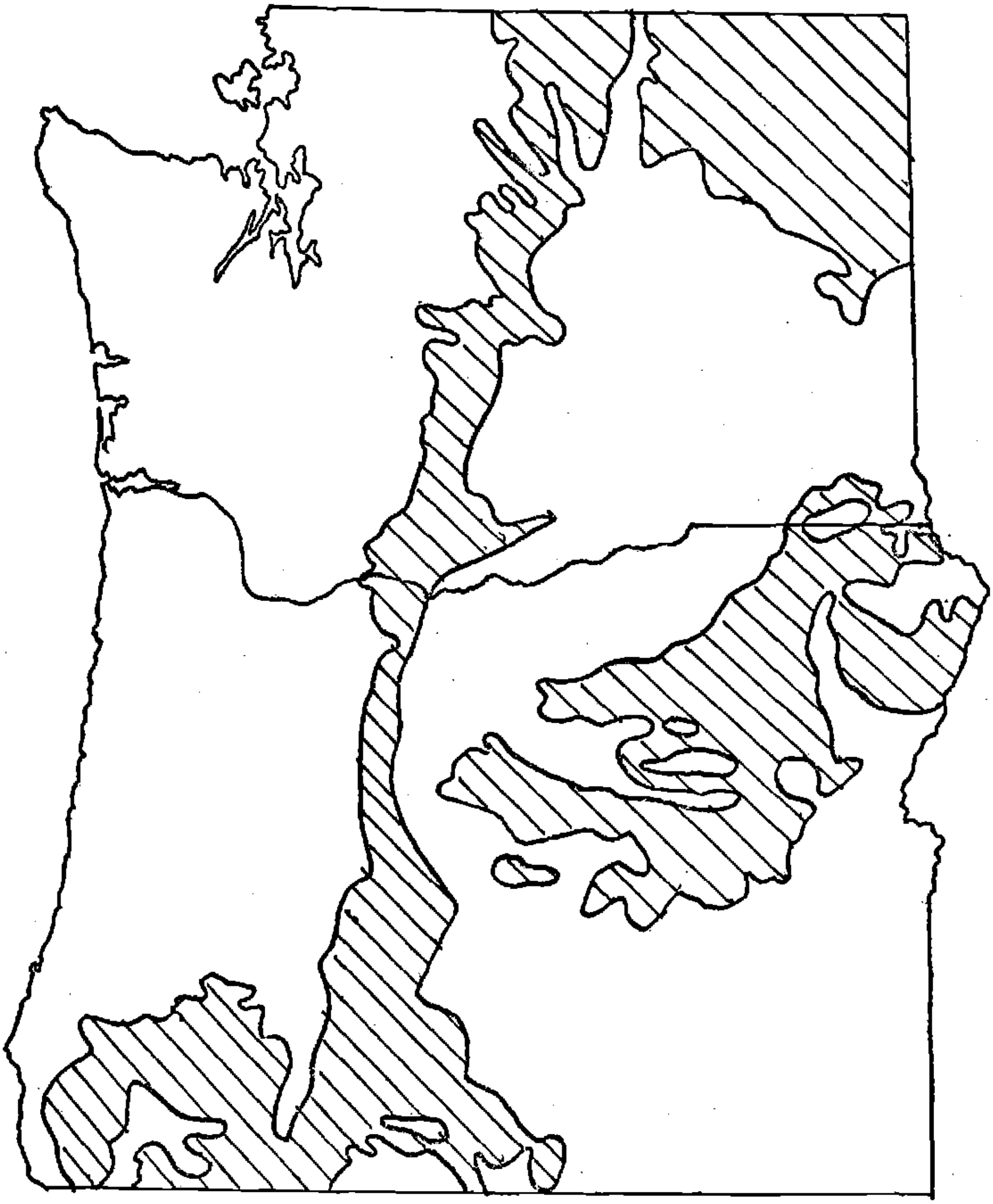

Figure 6. Distribution of Sphyrapicus thyroides.

pine occurs (Gabrielson and Jewett 1940). It is one of the most conspicuous birds of burned over country (Jewett et al. 1953).

g. *Sphyrapicus ruber*. *Sphyrapicus ruber* occurs west of the Cascades (Figure 7). It is a common resident of the Willamette Valley and the Coast Range and an uncommon resident on the west slopes of the Cascades into the Canadian zone. The preferred tree species of the red-breasted sapsucker are maples (*Acer* sp.), alders, willows, cedar, and hemlock (*Tsuga heterophylla*) (Larrison and Sonnenberg 1968). Soma altitudinal migration from the Cascades into the Willamette Valley and the Coast Range occurs.

h. *Sphyrapicus nuchalis*. The red-naped sapsucker is found east of the Cascades (Figure 8). It is migratory, arriving in April and remaining until October (Gabrielson and Jewett 1940). It is closely associated with aspens, being found in forests containing aspens in pure stands or mixed with conifers. On rare occasions it breeds in predominantly coniferous growth. Preferred tree species are alder, cottonwood, aspen, ponderosa pine, douglas fir, and larch (Larrison and Sonnenberg 1968).

i. *Melanerpes lewis*. The common characteristic of all the habitats used by lewis woodpeckers for breeding is openness (Bock 1970) (Figure 9). The requirement for openness is related to *lewis'* foraging methods--hawking for insects and gleaning in brush. A further requirement is for trees suitable for use as hawking perches

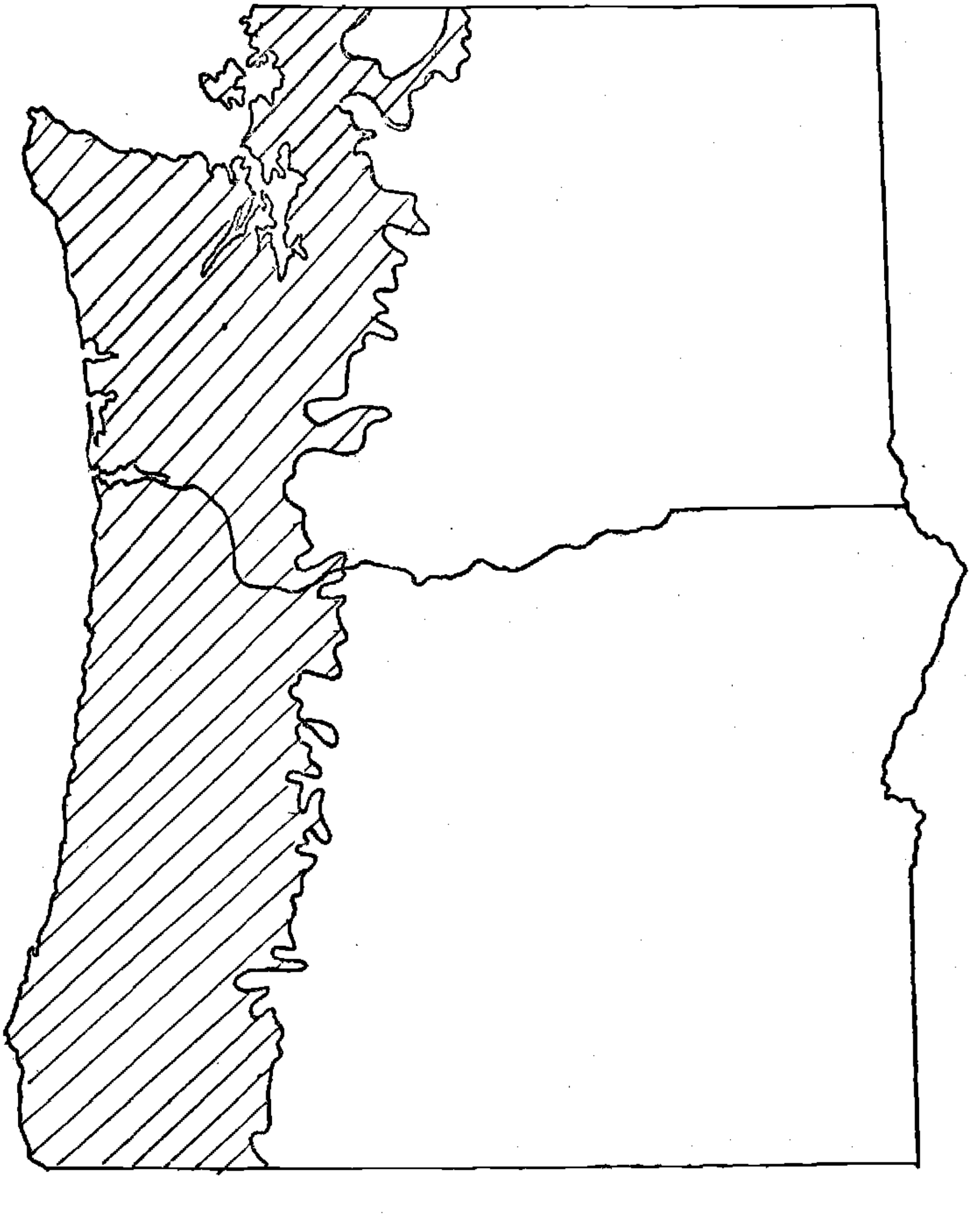

Figure 7. Distribution of Sphyrapicus ruber.

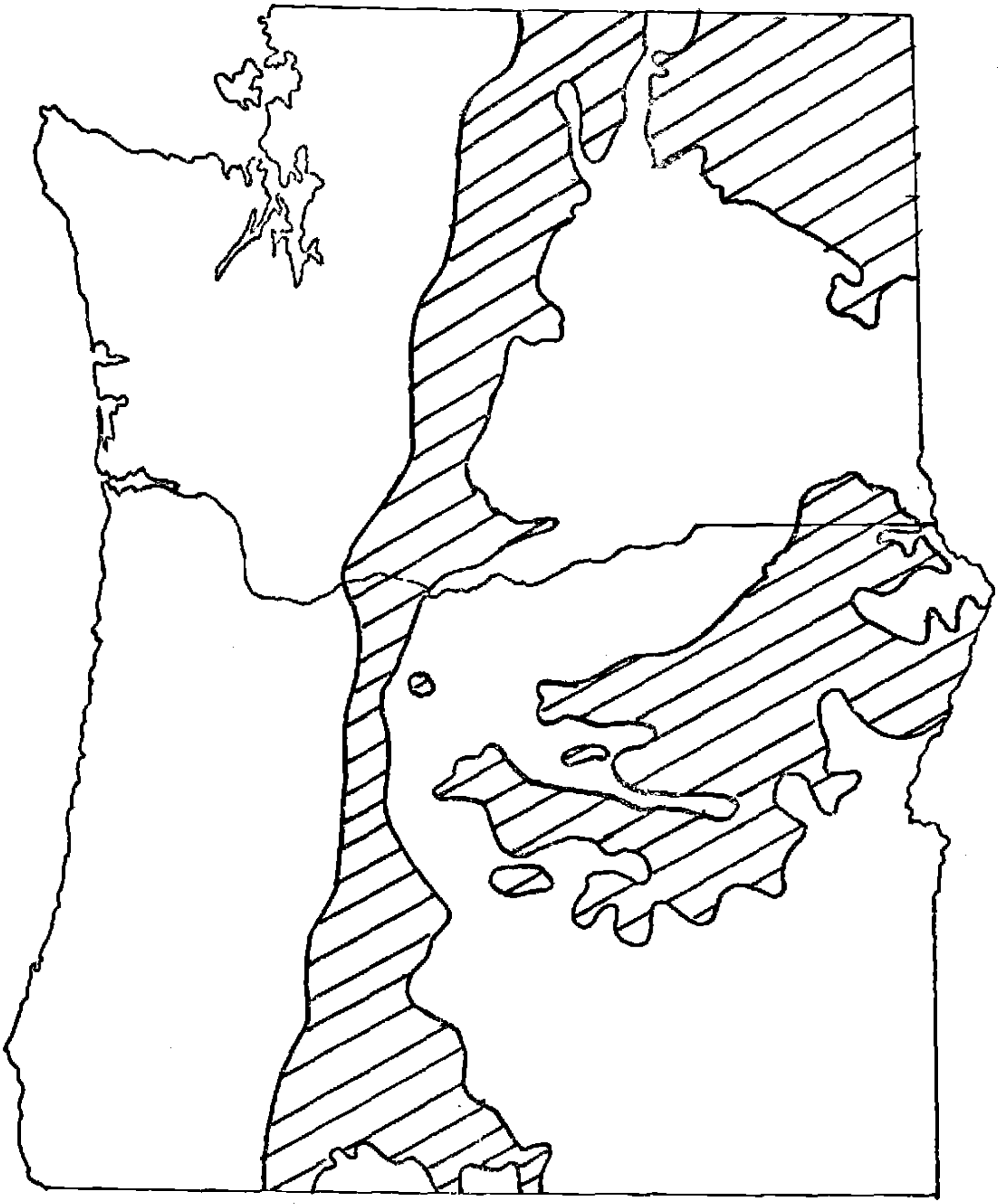

Figure 8. Distribution of Sphyrapicus nuchalis.

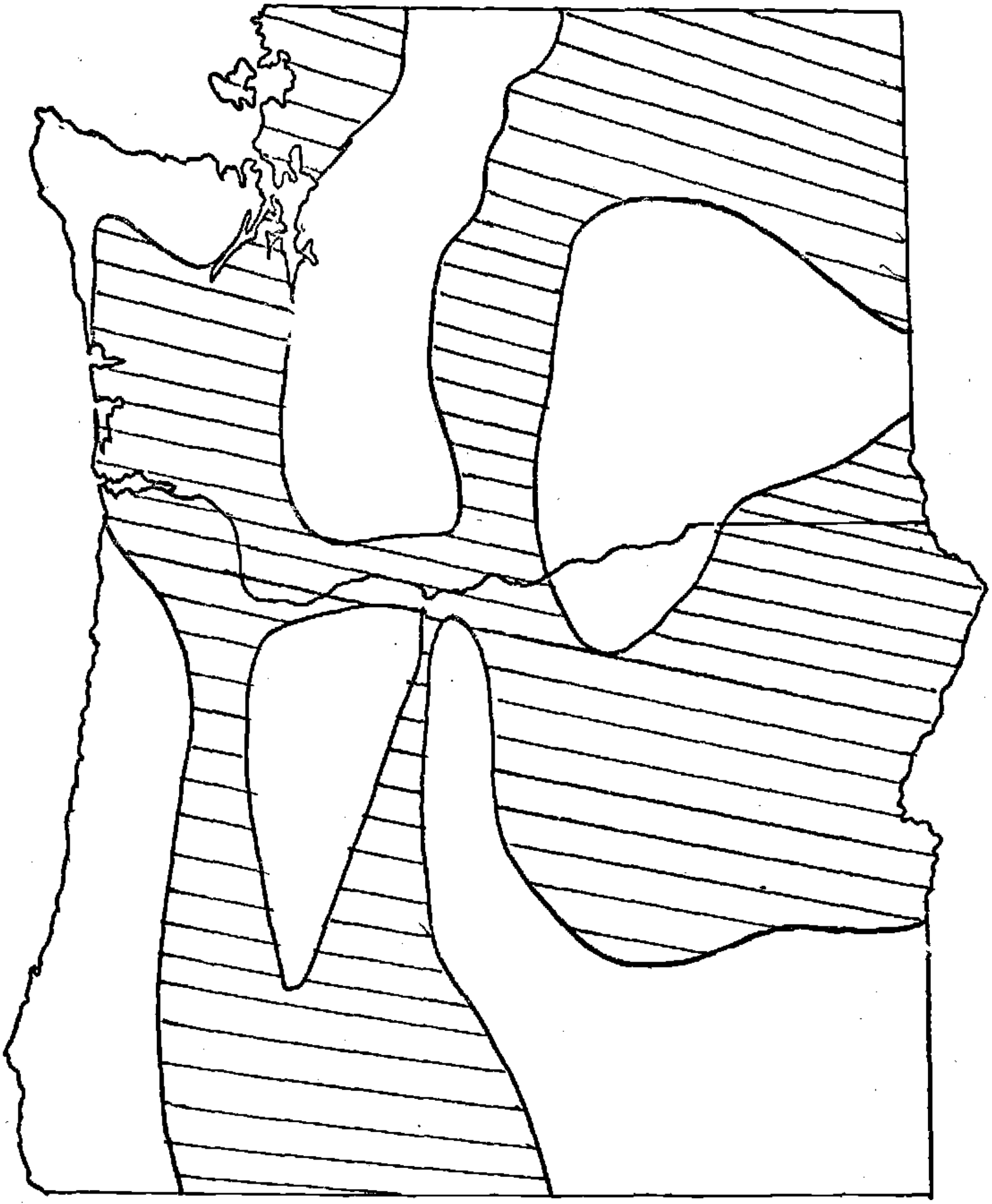

Figure 9. Distribution of Melanerpes lewis (Bock 1970).

and nesting. Lewis woodpeckers winter where there are oaks and where the weather is mild enough for some emergent insects to be available.

Park-like ponderosa pine is probably the lewis woodpecker's major breeding habitat. A critical element of this habitat is the brushy undergrowth consisting of such species as sagebrush (*Artemesia tridentata* Nutt.), golden current (*Ribes aureum* Pursh.), bitter brush (*Purshia tridentata* (Pursh) DC), and rabbit brush (*Chrysothamnus nauseosus* Britton) which support the insects upon which *lewis* feeds.

Another habitat is logged or burned coniferous forest, a habitat structurally similar to open ponderosa pine. Suitable habitat for lewis woodpeckers west of the Cascades is primarily of this type. Not all cut over or burned areas are utilized; those which do not revert to brush fields are not suitable habitat. In the cycle of decay and revegetation a burn may become good *lewis* habitat between about the tenth and the thirtieth years (Bock 1970). In the first years after a fire, dead trees become infested with wood boring insects. Woodpeckers such as three-toeds and hairys become common at this stage. Eventually dead trees begin to fall and if brush invades, the area becomes good *lewis* habitat.

At lower elevation, riparian woodlands are *lewis'* main breeding ground. Cottonwood groves are especially suitable. They are usually open; frequent changes in streams and riverbeds have left large numbers of trees which afford nest and roost sites. Insects are more numerous in riparian areas than in the drier uplands because the vegetation is more varied and lush.

Lewis woodpeckers will breed in oak woodlands if they provide enough openings. This openness is found most often along waterways or in savannah-like areas. The hardness of oak wood as an excavation site may be a factor limiting the breeding of lewis woodpeckers in oak woodlands. In some cases competition with acorn woodpeckers may prevent lewis from occupying oak woods (Bock 1970).

j. Melanerpes formicivorus. Acorn woodpeckers are permanent residents in oak groves or in mixed wood containing oaks. In Oregon formicivorus is expanding in range and abundance (Figure 10). In 1940 Gabrielson and Jewett listed Lane County as the northern limit of its range and the Rogue River as its center of abundance. In 1952 Walker reported seeing acorn woodpeckers in Corvallis. In 1954 Jewett commented that in the past 30 years there had been a noticeable increase of the acorn woodpecker in the Willamette valley. In 1965 Verner reported sightings in December 1960, August 1961, and December 1963, of acorn woodpecker in The Dalles on the south bank of the Columbia River. Reynolds (per. somm.) has seen this species near Hood River. Along both sides of the gorge from

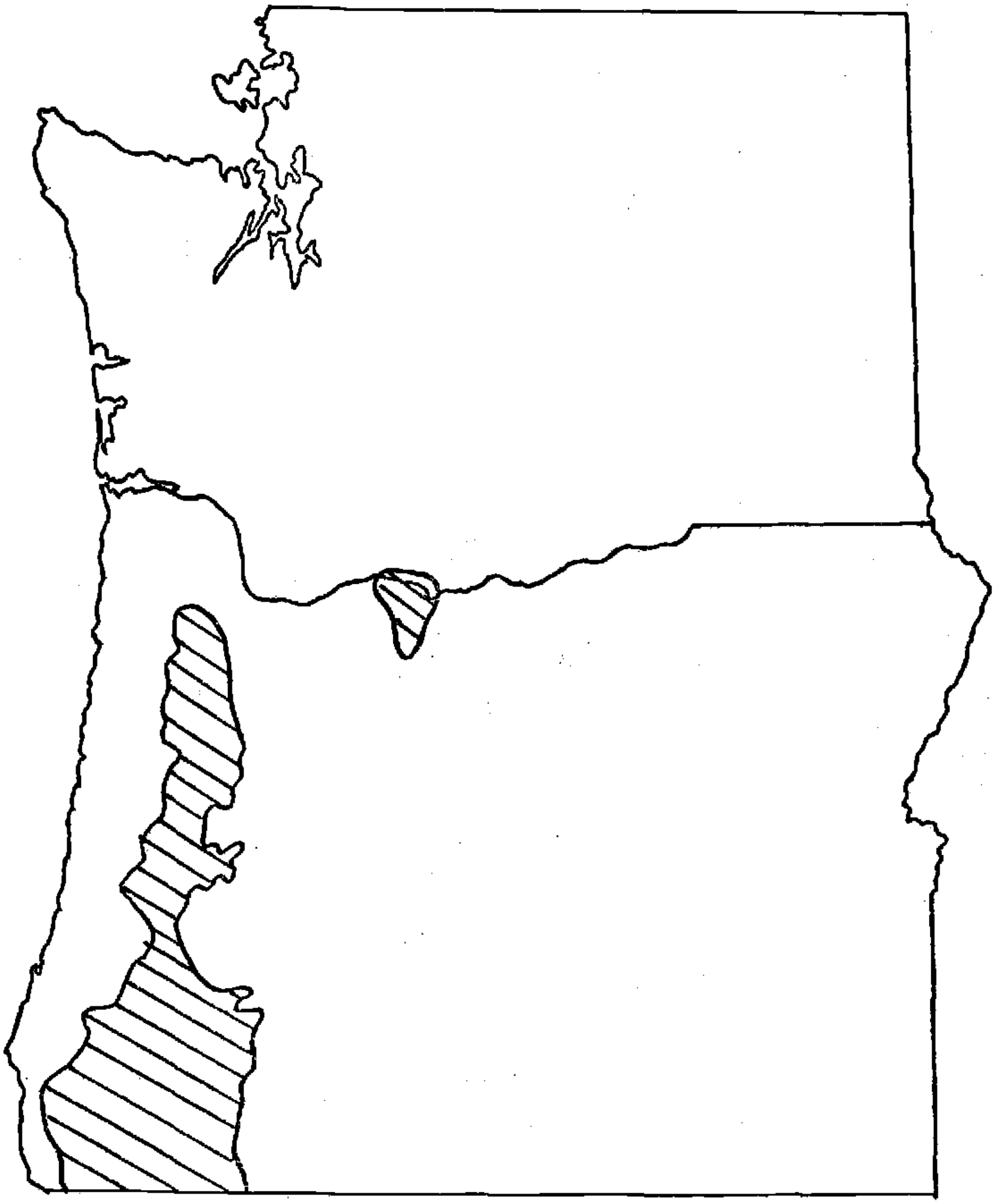

Figure 10. Distribution of Melanerpes formicivorus.

Hoof River east to The Dalles there are mixed forest of Pinus ponderosa and Quercus garryana which might provide suitable habitat for acorn woodpeckers (Franklin and Dyrness 1973). There are also oaks along the east flanks of the Cascades from 45° to 47° latitude and in the Puget Sound area of Washington. These areas may be potential habitat for the acorn woodpecker.

k. Colaptes auratus. The flicker is one of the more ubiquitous birds in the Northwest (Figure 11). Openness is the identifying characteristic of its habitat. It may be found foraging anywhere from fields to open forested areas, but it does not utilize dense growth. The flicker breeds from the coast to the limit of the trees; it occurs especially in wooded foothills or the banks of streams (Neff 1926). This species is also very common in residential areas. Flickers generally require trees suitable for excavating nest holes, but in treeless areas of eastern Oregon they will nest in posts or in holes in banks.

B. Foraging Patterns

1. Definition of Terms

Most woodpecker species have a large repetoire of feeding techniques. In the summer when insect food is plentiful, almost all species take advantage of abundant surface insects on trunks,

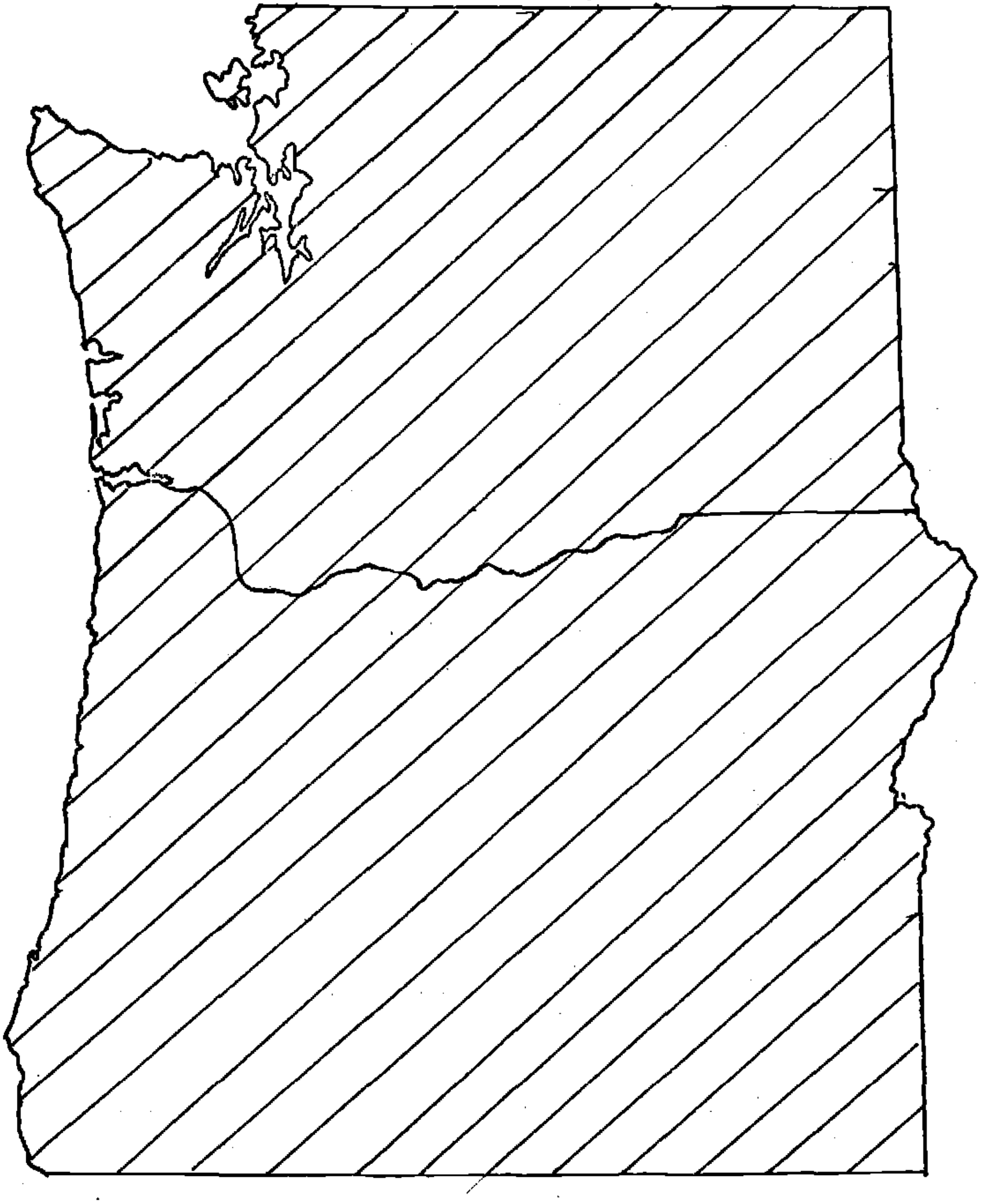

Figure 11. Distribution of Colaptes auratus.

branches, twigs, and the ground. In the winter when food is scarce the differences in foraging behavior become more pronounced. A terminology has grown up in the literature for describing the foraging techniques of woodpeckers. I distinguish eight foraging techniques.

Excavation: Excavation is the use of powerful blows to extract prey from deep within the wood. Synonym: digging.

Pecking: Pecking is the use of blows, rapid and continuous or relatively few, to locate and uncover prey beneath the bark or in superficial layers of the wood. It is loud and forceful. Synonyms: tapping, hammering, drilling, percussion.

Scaling: Scaling is the prying and knocking off of bits of bark with sidewise strokes to expose underlying insects. Little sound is produced by its performance. Synonyms: flaking, prying.

Gleaning: Gleaning consists of searching over limb and trunk surfaces for insects, and peering and probing into natural crevices and fissures. It is the most common woodpecker foraging technique in the summer when surface insects abound.

Sapsucking: Sapsucking is the eating of sap or cambium.

Flycatching: Flycatching is the capture of insects while in flight.

Ground Foraging: This method is distinguished because it requires a different agility than tree trunk foraging. Ground foragers hop or walk on the ground sometimes digging into the soil after insects, sometimes taking those on the surface.

Seed or Fruit Harvest: This category includes various techniques from acorn cracking to berry picking. The winter diet of many species is composed mainly of seeds or nuts.

2. Comparison of the Species

a. Picoides tridactylus and arcticus. The black-backed and northern three-toed woodpeckers are highly specialized for foraging on subsurface insects in tree trunks. Practically all of their food must be dug from beneath the bark, and usually in dead and decaying wood (Burt 1930). During an insect outbreak, Koplin (1967) found that tridactylus spent 93 percent of its foraging time on trunks, 6 percent on branches (> 2.5 cm diameter), and 1 percent on twigs (< 2.5 cm diameter). Three-toed woodpeckers prefer to forage on scaly barked trees: spruces, hemlocks, lodgepole pines, tamarack (Beal 1911).

The feeding pattern of three-toeds employs a minimum of vertical climbing and a maximum of static feeding. Spring (1965:463) writes that arcticus individuals are ". . . remarkably sedentary in their feeding. Pecking intently in the same area of trunk for long periods, they move slowly up the tree and may circle it several times over a short vertical distance." In Colorado Baldwin (1968a) found that tridactylus averaged 15 minutes at a feeding station before moving on.

b. Picoides albolarvatus. White-headed woodpeckers forage on trees having a very rough, scaly and deeply fissured bark (Bendire 1892). In southern California this species prefers coulter pine (Koch et al. 1970). In Oregon and Washington ponderosa pine and sugar pine are the only species which produce a scaly, deeply fissured bark. Ligon (1973) found that in Idaho white-headed woodpeckers foraged almost exclusively on ponderosa pine.

Albolarvatus is a quiet forager. It obtains much of its food by scaling on the main trunk and proximal branches of trees (Dawson 1923, Koch et al. 1970, Ligon 1973). In the winter white-headed woodpeckers feed mainly on pine seeds before the cones are open. (Wetmore 1964). Individuals cling to the side or even the bottom of a cone while chipping it open and exposing the seeds. In California Tevis (1953) estimated that a group of white-headed woodpeckers consumed 34 percent of 1,656 cones on 20 sugar pine trees.

White-headed woodpeckers probably drink more frequently than most woodpeckers (vanRossem and Pierce 1915, Grinnell et al. 1930, Ligon 1973). Ligon (1973) suggested this may be associated with the high proportion of vegetable matter in the diet.

Koch et al. (1970) working in southern California in the spring found that compared to females, foraging males moved about more rapidly, searched more superficially, and covered a larger proportion of a tree in comparable time intervals. Males spent about 20 percent of their foraging time on pine cones; females were not observed to forage on cones.

Ligon (1973) studying white-headed woodpeckers in Idaho from April through August, found no sexual differences in foraging behavior. During April woodpeckers foraged almost continuously on pine seeds. In June they foraged mostly in terminal needle clusters, presumably taking surface arthropods. In August they spent about equal time scaling on the lower trunk and foraging on pine cones.

c. *Picoides villosus*. The hairy woodpecker forages on a wide array of tree species, both living and in all stages of decay. Baldwin (1968a) described it as a fugitive feeder, moving quickly through the forest to ever new sources of food. Burt (1930) estimated that it spent 45 percent of its annual foraging time in pecking and excavating, 30 percent in gleaning and 25 percent foraging in places other than tree trunks. In Colorado, hairy woodpeckers commonly feed on fallen wood in early spring, taking advantage of insects that were protected all winter by snow (Baldwin 1968a). In Michigan, *villosus* will take sap in the spring when available but it does not prepare sapwells (Foster and Tate 1966).

In a study done in a ponderosa pine forest Stallcup (1968) found that in fall and winter hairy woodpeckers spent greater than 60 percent of their time foraging on seeds of cones on the upper crowns of ponderosa pine.

Kilham (1965) found that in New Hampshire the sexes of villosus tended to forage in different species of trees and that males excavated more than females which fed mostly in the superficial layers of bark by pecking and scaling. He described the excavations of the hairy woodpecker as similar to those of the pileated but smaller and shallower. In New York in winter, Kiesel (1972) found that the sexes foraged on a wide variety of different species of trees with different preferences for living or dead trees.

d. Picoides pubescens. Downy woodpeckers forage mainly on deciduous growth. They forage in brush as well as trees, and are adept at climbing on small branches and twigs. The small size of the downy makes it energetically feasible for it to forage on small but abundant insects such as aphids and coccids (Beal 1911). Pubescens occasionally flycatches (Lawrence 1966); it does a considerable amount of sapsucking (Foster and Tate 1965).

In the winter downy woodpeckers forage in mixed species flocks of small birds, such as nuthatches, kinglets, and chickadee (Morse 1970, pers. obs.). Downy woodpeckers may compete for food with these species more than with other woodpeckers. Its habit of flocking with these small birds may be evidence of competition with them. Morse (1970) found that all members of mixed species flocks he studied overlapped in foraging behavior with at least one other species in the flock. Subordinate species usually retreated to the foraging station or technique they were best adapted to in the presence of dominants. Thus the dominants obtained a more predictable portion of the food supply and the subordinates avoided hostile interactions which waste time and energy. In the flocks Morse studied downys were subordinate.

Most studies have shown that downys forage on all parts of the tree (Morse 1970, Jackson 1970, Beal 1911). However in his study Koplin (1967) found that downys spent almost 100 percent of their foraging time on twigs less than 2.5 cm in diameter. It may be significant that the study area was the site of a spruce beetle infestation and there were high densities of hairy and three-toed woodpeckers present. In the presence of these species the downy woodpecker probably retreated to its area of specialization, the smaller branches and twigs. Hairy woodpeckers spent 12 percent of their time foraging in twigs and the three-toeds spent only 1 percent foraging in twigs. Thus downy woodpeckers could reduce competition by restricting its foraging to small twigs.

Kilham (1970) working in New Hampshire in the winter, found that when alone each sex would feed in the same manner but when male and female foraged together the male tended to feed on the upper trunk, limbs and branches while the female fed on the main and lower parts of the trunk. Kisiel (1972) working in New York state during the winter found that males worked more on twigs and branches and females more on trunks. Males spent more time pecking and females more time gleaning. The sexes also exhibited some difference in tree species preference.

e. Dryocopus pileatus. Tanner (1942) estimated that the pileated woodpecker obtained 72 percent of its food by excavating and 23 percent by scaling. Carpenter ants compose about 40 percent of its diet (Beal 1911). These insects penetrate upwards from the base of a tree into the heartwood. Pileateds can unerringly locate contaminated trees and excavate the wood to reach a colony (Wetmore 1964).

Twenty percent of the pileated's diet is beetle larvae excavated from rotting wood (Beal 1911). When a tree dies insects living beneath the bark invade, reach their peak of abundance in about two years and decrease and disappear. Insects that bore within the wood follow, and inhabit the gradually decaying wood until the tree has almost completely rotted away. Pileateds are capable of literally tearing apart a rotting log to get at these insects. Their excavations may be 30 cm long, 10 cm wide, and 20 cm deep (McAtee 1911).

Hoyt (1957) reported that in the fall pileateds feed on many species of fruits, seeds, (especially seeds of Rhus sp.), cambium and mast. Michael (1928:157) described a pileated eating dogwood berries. It would ". . . flutter clumsily up to a branch containing berries, clutch the branch firmly with its strong feet and then drop, to swing like a pendulum."

f. Colaptes auratus. Flickers forage almost exclusively on the ground, especially on lawns and meadows. They dig with their bill, tearing up anthills and catching the inhabitants with their tongue (Gabrielson and Jewett 1940). More than half of the yearly diet of the flicker is ants (Beal 1911). In the fall auratus consumes acorns, grains, and other seeds (Beal 1911). Flickers often forage in flocks, frequently with robins and blackbirds.

g. Melanerpes lewis. Lewis woodpeckers spend little time foraging on tree trunks in the traditional woodpecker fashion. During summer, lewis woodpeckers spend about 60 percent of its foraging time flycatching, 30 percent ground-brush foraging, and 10 percent gleaning insects from trunks and branches of trees. During the winter about 70 percent of the foraging time is spent on acorn harvest and storage, 15 percent flycatching, and 13 percent gleaning insects from the surface of tree trunks (Bock 1970).

Flycatching is carried out from a scanning perch which varies from a low stump or fence post to the tops of the tallest trees depending upon the type of insects lewis is hunting. Neff (1926:92) describes the hawking behavior:

> After perching for some time upon the top limb of some dead tree the bird will suddenly dart into the air, perform several peculiar circular gyrations, then spreading its wings horizontally in the manner of a hawk it will soar back to the identical perch it quitted.

The gyrations are in response to the insect's excape behavior of suddenly dropping as a predator approaches (Bock 1970). When insect density is high, lewis will remain in the air taking one insect after another without returning to its perch. Twelve percent of the flights observed by Bock were of this type. Lewis woodpeckers tend to concentrate on one or a few insect species which are particularly abundant, and they often feed in aggregations (Bock 1970).

Foraging directly on the ground or in low brush involves scanning from low stumps, bushes and the sides of tree trunks for insects moving over the ground. Lewis woodpeckers move with agility over the outer branches of shrubbery.

During the winter, lewis lives on cached acorn meats and any insects which emerge. Each individual harvests, stores and maintains its own cache which is defended from other birds and mammals. The nut meats are removed from the shell on a special shelling perch, which Bock (1970) calls an anvil, before they are stored. The nuts are pressed into natural crevices in a tree trunk or limb or, sometimes in a utility pole.

h. Melanerpes formicivorus. Acorn woodpeckers are the most social of North American woodpeckers, living in communal groups of two to ten birds. Food gathering and storage are accomplished jointly by all members of a group.

Flycatching is the major foraging method of the acorn woodpecker during the breeding season (MacRoberts 1970). Sapsucking begins sometime in spring and reaches a peak in June and July. The birds have one or two sap trees which they defend from other birds. Small holes, 5 to 15 mm in diameter and 3 to 19 mm deep are continuously being drilled on the upper surface of middle and upper canopy branches. In mid-summer every sap-hole may be visited by a member of the colony 4 to 10 times per hour (MacRoberts 1970).

Sapsucking ceases in August and September when green acorns become an important food source. Storing begins in mid-September when the acorns become ripe. Acorns are stored whole in holes prepared in the surface of oaks. These stored acorns are the major source of food until spring when insects begin emerging and the sap rises in the trees (MacRoberts 1970).

i. Sphyrapicus thyroides. During the breeding season the williamson's sapsucker obtains most of its food by gleaning. In a study of feeding habits in Colorado, Stallcup (1968) never observed thyroides pecking in the bark for insects. Individuals foraged mainly on trunks of live ponderosa pine for ants. After proceeding up the trunk a bird usually hopped on a lateral branch, progressed along the upper surface a short distance, and then flew to the base of another tree.

The williamson's sapsucker migrates to the southwest during the winter; nothing is known of its winter feeding habits. After returning in early spring thyroides feeds largely on sap making a characteristic series of square holes, usually in ponderosa pine although other species are used (Guiget 1954). Stallcup (1968) found that in late summer williamson's sapsucker forages mainly by removing small sections of bark from the main stem of ponderosa pine and eating the underlying layer of phloem.

j. Sphyrapicus ruber and nuchalis. Foraging techniques of ruber and nuchalis include sapsucking, flycatching, gleaning, and pecking (Burt 1930). In Ontario and Michigan, sapsuckers of the [varius] superspecies drink dilute sap as it rises in the spring (Tate 1973, Lawrence 1966). During the breeding season foraging is mainly by flycatching and gleaning (Burt 1930, Spring 1965, Lawrence 1966). Ruber and nuchalis usually forage mostly on one or two trees within 90 meters of the nest site (Howell 1952).

Sapsuckers initiate sapwells by drilling primary bands of small holes in horizontal rows (Tate 1973). These bands are exploratory and are drilled in many trees. Productive sapwells are expanded by drilling progressive columns above and below the initial band.

3. Sapsucking

Seven of the twelve species of woodpeckers in the Northwest have been observed drinking sap: *tridactylus* (Bent 1939), *villosus* (Nickel 1956, Kilham 1965, Foster and Tate 1966), *pubescens* (Bolles 1891, Nickel 1956, 1965, Kilham 1964, Foster and Tate 1966), *thyroides* (Bent 1939, Stallcup 1968), *ruber* and *nuchalis* (Bent 1939, Howell 1952), and *formicivorus* (Fisher and Peterson 1964, Hadow 1970). Of these species, all but *villosus* have been observed drilling sapwells. Sapsuckers also eat the phloem fibers, rays, sieve tubes and parenchyma: the soft inner bark which is collectively called bast.

Sap is obtained from both gymnosperms and angiosperms by tapping into the phloem. Phloem sieve tubes are formed in early spring and are filled with sap under turgor pressure. They form a layer often less than one millimeter thick. In angiosperms, with decreasing photosynthetic activity in the fall, the sugar content of the sap decreases and the turgor pressure in the sieve tubes is slowly reduced until the cells collapse. Nutrients are stored in relatively inactive forms in storage cells in the roots and stems. Phloem sieve tubes of conifers do not collapse; in the winter on cold days the phloem sap freezes within them. On warm days photosynthesis occurs and sap flows (Kilham 1956).

Early in spring sapsucking is restricted to conifers because deciduous trees are still dormant. The birds feed extensively on bast. Later in the spring angiosperms become active and begin reconstituting the sap from winter stores. The sap moves up the tree in copious amounts but the sugar concentration is low, about 3 to 4 percent (Tate 1973). The sapsuckers remain at the sapwell for hours; the cloaca is emptied about once a minute of a clear faintly brown liquid (Tate 1973). During the summer the volume and quality of the sap are related to the rate of transpiration of the tree. When trees are fully leaved and photosynthesis is at a peak, sugar concentration of the sap is about 20 percent (Kilham 1964).

4. Food Defense

a. Defense of Sapwells. [Varius] sapsuckers will displace individuals at their sapwell when arriving to feed but otherwise they do not defend them. Foster and Tate (1966) identified 22 families of insects, 20 species of birds, and 5 species of mammals which fed regularly at sapwells. Frequent visitors to the sapwell establish an interspecific hierarchy at the sapwell. Foster and Tate (1966) determined the ranking from most to least dominant to be: red squirrel, sapsucker male, sapsucker female, downy male, sapsucker juvenile, downy female, nuthatch, hummingbird.

There is no evidence that williamson's sapsuckers establish sap trees to which they return regularly. Stallcup (1968) indicated that

Williamson's sapsuckers were seeking bast, a non-renewing resource, rather than sap.

Acorn woodpeckers exclude all intruders from their sap trees during summer when they are feeding on sap. MacRoberts (1970) reported nuttall's woodpeckers (71 interactions) and anna's hummingbirds (31 interactions) as the main intruders at the sapwells of one group of acorn woodpeckers.

b. Defense of Mast. During winter individual lewis woodpeckers store acorns and vigorously defend their caches (Bock 1970). Bock found that in winter lewis woodpeckers spent 42 percent of their time at their storage sites; about half of this time was spent perched at the cache, which discouraged intruders. In 113 hours of observation on wintering areas Bock observed 146 interactions at acorn caches; the primary intruders were acorn woodpeckers (43), lewis woodpeckers (26), plain titmouse (*Parus inornatus*) (16), flicker (14), and nuttall's woodpecker (14).

Bock (1970) hypothesized that the more frequently a species attempted to rob a lewis woodpecker the greater the competition between them. Hadow (1973) noted that the level of aggressiveness of an individual lewis woodpecker varied with the species of the intruder and the abundance of available food. He wrote (Hadow 1973:220) "Differential defense of stores conserves energy since the greatest effort is spent against the most important competitors." In contrast, in his study of acorn woodpeckers MacRoberts (1970) found that heterospecifics that were supplanted were not necessarily involved in food competition with the woodpeckers; no discrimination was made between intruders.

Acorn woodpeckers, which display group defense of acorn caches exclude all intruders from caches indiscriminately, even those which pose no competition. Lewis woodpeckers have become more fine tuned. This may be because they have a more limited budget than acorn woodpeckers; each individual has to collect and protect food stores individually, and there has thus been selection to eliminate the wastage of time and energy entailed in chasing off non-competitors.

C. Communication

1. Auditory Communication

a. Introduction. Auditory communications in woodpeckers include vocalizations and mechanically produced sounds. Woodpeckers have no song, only calls. Following mainly the work of Short (1971a) and Lawrence (1966) I have placed woodpecker calls into five categories (Table 3). There are intergradations between types of calls and variations occur depending on circumstances and the internal state of the bird. Mechanical sounds used by woodpeckers include drumming and ritual tapping.

Table 3. Summary of words used to describe woodpecker calls.[1]

	Location, Low Intensity Alert	High Intensity Alert	Threat, Location, Territory	Courtship, High Intensity Threat	Appeasement
P. arcticus	tchuck, kip, chet	kuk-kuk, rapid chet	wreo	kick-er-uck-tchick, pet-pet-wreoo	--
P. tridactylus	queep, quip	--	rattle	choi-yoi-yoi	--
P. albolarvatus	wiek, pitit	cheep-eep-eep, yip-yip-yip	chick-it up	witt-witt	--
P. villosus	klick-keck-keck, peek	klick-kekherrr-kerr-kerr, prrrit	klick-klick, rattle	eeyick-yick-yick, queek	eejew-jew-jew, tewk
P. pubescens	tick-tick-tick, pit, spatter	tickirrrr, chip, kick	chrrr, whinny, rattle	tchick-tchick-tcherrick, queek, check check	tut-tit-wi-tut-it, tewk, chirp
D. pileatus	random cuks	6-8 high pitched cuks with a terminal one of lower pitch	woick-woick	G-waick-G-waick	hn-hn
S. thyroides	whang, whether	explosive cry, cheeer	k-k'-rrr	--	--
S. ruber and *nuchalis*	view	hoarse view	owee-owee, wee-yah, weetick-weetick	juk-juk	soft mjuk
M. formicivorus	clee-ep, clee-ep	whack-up, Jacob	chak-a, chaka, chak	karrit-cut	low chatter or purr
M. lewis	yick (male) yick-ick (female)	--	churr call	chatter call rapidly descending series of short squeaks	--
C. auratus	pee-up	kakaka-kakaka	keck-keck, klee-yer, wick-wick	wee-cha, wee-cha, we-cup, flick-ah	jew-jew-jew

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[1] References: Noble (1936), Bent (1939), Hoyt (1957), Kilham (1959d, 1960), Lawrence (1966), Bock (1970), Bock et al. (1971), Short (1971a).

b. Vocalizations. (1) Location and low intensity alert: This call is given by woodpeckers when slightly alarmed by the approach of an intruder or by sudden noises or movements at a distance. The same notes are employed as location calls by members of a pair.

(2) High intensity alarm: This call is generally a sharper, more intense version of the low intensity alert. It is uttered more rapidly. During nesting the high intensity alarm call is used as a warning call to silence the nestlings.

(3) Threat, territorial defense, and self-announcement: This call usually elicits a response from conspecifics within hearing range. Individuals may respond with the same call, signal by drumming, or fly in. This call expresses threat of moderate intensity. It is used during encounters and in proclaiming territories.

(4) High intensity threat, and courtship: These calls are harsh and loud, conveying more aggression than the previous three types of calls. They are often uttered by displaying birds.

(5) Appeasement notes: These are soft calls often uttered by members of a pair when close together, and between intensely displaying birds of the same sex.

c. Mechanical Sounds. (1) Drumming: Drumming is a loud series of sounds produced when a woodpecker's bill hammers on a resounding object (Lawrence 1966). The function of drumming is similar to that of song in passerines. Individual woodpeckers show distinct preferences for particular drumming sites. The sound is rhythmic and distinct. A species can be recognized by its drumming, but individuals generally cannot (Lawrence 1966). The number of individual taps in a drum depends on the circumstances and probably on the time of year (Short 1971a).

Short (1971a) reported a ready reaction to the drumming of other species in nuttall's, downy, and hairy woodpeckers. He concluded that differences in cadence and duration of drum is unlikely to play a role in species recognition. Lawrence (1966) suggest that drumming is important in pair bond formation.

The drum of Picoides species has a simple rhythm consisting of single rolls repeated rapidly in a series of varying length (Short 1971a). Arcticus generally drums in bursts of approximately two second duration, repeated at intervals of 30 to 40 seconds with a dimunition at the end of each burst (Kilham 1966). Villosus executes rolls of 12 to 15 taps two to five times a minute. Commonly two individuals will drum to each other either alternately or simultaneously (Lawrence 1966). The rate and intensity of the drum of pubescens is variable, with bursts about 1-1/2 seconds long repeated at the rate of 9 to 14 bursts per minute; up to 24 bursts per minute occur in intense situations.

The drum of ruber and nuchalis is a rolling tattoo (Jewett et al. 1953). It is 3 to 5 seconds in duration, starting with a steady roll 1 to

2 seconds long followed by a series of loud taps at irregular intervals for 2 to 4 seconds. A verbal representation is drrr - a - da, da-da, da. Thyroides uses the same rhythm but with a slightly slower tempo.

Pileatus produces very loud drums in bursts lasting about three seconds. The bursts are delivered at intervals of 40 to 60 seconds, 4-7 times in a row. Vickers (1914:16) describes the drum of the pileated:

> . . . making a pass or two, as if about to begin as a skillful penmen makes a preliminary flourish, he came suddenly and almost savagely down on the limb; and though the blows were slowly and lightly delivered at first, they increased in speed and force one by one to the highest power, whence they diminished to the close. Thus his roll was composed of a dozen strokes delivered as an ascending and descending climax. These tones were of a peculiar rich xylophone quality, echoing in ever widening and pleasing circles off through the wood.

Vickers could hear the drum of this bird 2 km away in his house with doors and windows closed.

The drum of auratus starts with a roll of 6 to 8 taps often followed by one or two additional rolls of 3 or 4 taps (Lawrence 1966). Each burst lasts for about one second, coming at intervals of 10 to 40 seconds (Kilham 1959b). Two birds may drum alternate or perform in unison.

(2) Ritual tapping: Ritual tapping is a soft tapping used in communication between members of a pair. It is significant in pair bond formation and in synchronizing the excavating activities of the

pair (Lawrence 1966).

2. Visual Communication

All woodpeckers have approximately the same repertoire of movements which they employ in display. However, the style is variable and each species has distinctive combinations of movements and particular displays which predominate.

Three-toed woodpeckers often emit continual vocalizations during display (Baldwin 1960). Kilham (1966) observed a wing spreading display. With wings spread the bird reared back and assumed a rigid stance from which it seesawed back and forth. In intense threat the wings are raised upward and extended over the back.

Displays of villosus are characteristically vigorous and interspersed with periods of fixed immobility (Lawrence 1966). Feather erection is elaborate including raising of the nape spots, erect contour feathers and raised crest.

Lewis has pink and silver feathers on its throat and breast which are erected during display. It is the most aerial of North American woodpeckers and its displays are predominantly flight and wing spreading displays. The wing spreading display is an exaggerated extension of the wings laterally and dorsally away from the body. The head is depressed and the silver feathers of the throat and breast puffed out. During circle flight the bird circles in a smooth glide with the wings extended and held at an unusually high angle (Bock 1970).

The most prominent movement of auratus is tail spreading, which exposes the bright undersurface of the tail. During display the heads of the flickers are in constant motion. Their displays are commonly a composite of head bobbing and head swinging. The movements are smooth describing a circular up and down path (Lawrence 1966, Short 1971b). Flickers often hop from one branch to another while displaying (Lawrence 1966).

D. Reproduction

1. Territoriality

a. Territory Size. In the spring most pairs of woodpeckers establish breeding territories. The nest tree itself is a strong focal point of the territory. Lawrence (1966) distinguished two types of territories established by downy and hairy woodpeckers, flickers, and sapsuckers: the area immediately surrounding the nest and a larger more loosely defended feeding territory. Pairs aggressively defended the immediate area from all intruders regardless of species. In the loosely defended territory, non-picids were tolerated, and feeding territories of heterospecific pairs of woodpeckers often overlapped. The defended area around the nest tree had a radius of 6 to 15 meters. Loosely defended territories had flexible borders. Lawrence (1966) estimated that the sapsucker's territory was about 2 hectares. Hairy and downy woodpecker territories were 2 to 3 hectares.

Kilham (1960) estimated that the territories of hairy woodpeckers in New Hampshire were roughly 500 meters in length; they had borders which were ill defined in most directions. Howell (1952) found that the size of the territories of ruber and nuchalis varied from 45 to 90 meters in radius. The size of the territory seemed to depend on the density of trees. The foraging range of the birds was much larger than the defended territory, extending at least 180 or 275 meters from the nest, provided that the territory of another bird was not penetrated. Baldwin (1960) and Koplin (1967) found that the average territory of the northern three-toed woodpecker was about 43 hectares during a spruce beetle outbreak. A pileated woodpecker territory in Florida was at least 275 meters long (Kilham 1959d).

Breeding lewis woodpeckers are opportunistic in foraging habits. They are protective only of their immediate nest site and do not defend a feeding territory because of the diffuse and sporadic nature of their food supply.(Bock 1970).

Acorn woodpeckers are colonial. Members of each group supplant heterospecifics from their acorn storage and sapsucking trees, the acorn bearing oaks from which they gather acorns, their roosts and nest holes, and occasionally from anvils and hawking perches. Conspecifics of a different group were completely excluded from the territory which encompassed about 2 hectares (MacRoberts 1970).

b. Interspecific Territoriality. There is evidence of interspecific territoriality in some woodpecker species. Selander and Giller (1959) demonstrated that two species of woodpeckers in Texas, Melanerpes carolinus and M. aurifrons, held mutually exclusive territories. Howell (1952) mentioned that sapsuckers showed aggressive behavior toward trespassing picids of similar size such as hairy woodpeckers. Acorn woodpeckers and lewis woodpeckers establish interspecific territories during winter (Bock 1970). Lewis woodpeckers and the red-headed woodpeckers are ecological equivalents, inhabiting western and eastern North America respectively. In the region of overlap in Colorado they hold exclusive territories (Bock et al. 1971). Territories of hairy, downy, and nuttall's woodpeckers generally overlap in California (Short 1971a); however Short noted that behavioral interactions occur among the three species and suggested that interspecific territoriality may occur in unfavorable habitat.

One would expect natural selection to favor ecological divergence of sympatric species because interspecific territoriality is demanding of time and energy (Orians and Willson 1964). A lack of ecological divergence may simply mean that insufficient time has elapsed for the divergence to be completed. In the Northwest two pairs of ecologically similar woodpecker species may have evolved in isolation and more recently come into sympatry: tridactylus and arcticus and formicivorus and lewis.

Species recognition is based on auditory and visual characteristics. Cody (1969) suggested that similarities in coloration, voice, or both may promote spatial separation among sympatric species. Woodpeckers are rather similar in plumage patterns. Dryocopus pileatus is strikingly similar to Campophilus principalis, but the two species have evolved from different phylogenetic lines (Cody 1969). In coloration pubescens is a smaller version of villosus. The phylogenetic history of the two species does not warrant this similarity (Short 1971a). These two examples may be cases of convergence to facilitate interspecific territoriality.

Territorial displays of woodpeckers have common components performed in certain combinations and in a characteristic style by each species (Short 1971a). Incidents of interspecific display are reported in the literature (Gibbon 1966, Tanner 1942, Hoyt 1948, Howell 1952).

c. Nesting in Close Proximity. Hole nesters probably face a shortage of nest sites (Section IV. B.). This limited resource is often spatially distributed in clumps. Snags, dead-topped trees, fungus infected trees, etc. are frequently found in groups, for instance at the site of an insect outbreak, in an old burn, or a dry riverbed. Potential nest sites are in high demand and in such areas many woodpeckers may nest within a few meters of each other. These exceptions to territorial behavior are often cited in the literature.

Hoyt (1948) observed the successful nesting of a pair of pileated woodpeckers and a pair of flickers in two holes on opposite sides of a tree with cavities separated on the inside by only a few centimeters of wood. Schmenitz (1964) observed a pileated woodpecker and a flicker nesting in the same utility pole. Currier (1928) found three holes occupied by lewis in each of two trees less than 400 meters apart. Smith (in Bent 1939) reported at least eight nests of the white-headed woodpecker within an 800 meter radius. Fleming (1901) found black-backed three-toed woodpeckers nesting in a colony in which there were 6 or 7 nests each cut into the trunk of a living cedar.

2. Pair Formation

a. Introduction. Woodpeckers generally remain paired for life (the acorn woodpecker probably does not pair (Ritter 1938)). This fidelity is probably due to strong site tenacity exhibited by both sexes. Resident species often maintain a pair bond from November or December through July. Migratory species pair upon return in the spring and pairs break up in July after nesting (Lawrence 1966).

If both partners of a previous pair survive, mate selection is a product of site tenacity. If one member of a pair dies over the winter, the other member, male or female, claims the territory and attracts a mate with its drumming. In the case of birds mating for the first time, the male is usually the first to take up residence on a territory. It is the territory and not the bird that is selected by the second member of a pair (Lawrence 1966). Once the two birds have established residence on a territory the pair bond is developed through repeated displays.

b. Drumming. Drumming is a frequent activity during the period of pair formation. The territorial call has a similar function but it is a more intense display prevalent in territorial proclamation at a distance and not so often used in actual encounters as is drumming (Short 1971a). It is much less common than drumming in most species. However, the lewis woodpecker drums infrequently, using instead the territorial call to attract a mate and proclaim a territory (Bock 1970).

c. Courtship. The drumming of woodpeckers serves as a summons; the encounter of two or more individuals results in a round of displaying. Participation of more than two individuals in territorial and coutship displays is characteristic of many woodpeckers (Lawrence 1966, Howell 1952, Noble 1936, Evelyn Bull, pers. comm.). The frequency with which display occurs depends on the number of woodpeckers of the same species in the area. Participants include transients, individuals with designs on one of the two resident birds and birds from neighboring territories (Lawrence 1966).

d. Copulation. Copulation usually begin three or four days before nest excavation is completed. Frequency of copulation reaches a peak during egg laying and declines during incubation (Lawrence 1966). Woodpeckers have an unusual way of copulating which is attributed to their specialized anatomy, particularly their stiff tail feathers and short legs. The male usually approaches by hopping up to the female but in some cases hovers down upon her back from above. He then slides down her left side holding on to her with his feet. He swings the whole posterior part of his body under the female's uplifted tail with his own tail pressing against her right flank.

3. Selection of the Excavation Site

It would benefit a woodpecker to be able to distinguish good excavation sites from poor ones. Picids and other excavators may have highly specific methods of selecting excavation sites. Foresters have developed methods of predicting the patterns of decay within a tree from external signs such as conks and cankers (Shigo and Larrison 1969). Woodpeckers may use similar signs. There is some evidence that conks of *Fomes ignarius* act as a proximate factor in selection of a nest tree by yellow-bellied sapsuckers (Kilham 1971).

Stage of decay is probably a factor in selection of a nest tree. Erskine and McLaren (1972) found that *nuchalis* would cut through greater thicknesses of sound wood to reach a rotted heartwood than would *auratus*. The species of the nest tree is also significant, probably more so in some picids than in others. Haapanen (1965) found tree species important in nest selection by Finnish woodpeckers. Table 4 presents data on preferences for species of nest tree of woodpeckers in the Northwest. The figures were compiled by recording references in the literature to tree species in which a nest hole was found. Undoubtedly preferences of woodpeckers for tree species vary geographically depending upon availability of trees. Thus Table 4 is a rough approximation probably more indicative of what trees make good nest trees than preferences of individual woodpecker species.

Haapanen (1965) found the diameter of the tree to be a significant parameter of nest site selection, There are probably correlations between tree diameter, height of the cavity and size of the bird. Estimates of height of nest caivities of Northwestern woodpeckers were calculated from records in the literature (Figure 12).

Lawrence (1966) noted that cavities in trees surrounded by tall growth tend to be bored at greater height than those in trees in more open places. She attributed this greater height to a need for light within the hole. Her data also indicated a tendency for openings of cavities to fact south and east. Conner (1973) found that the entrance of all 69 of the nest cavities he studied were excavated so that their openings were directed slightly downwards; the average was about

Table 4. Tree genera or species used by Northwestern woodpeckers for nesting. Figures are a tabulation of nesting records in the literature.[1]

	P. arcticus	*P. tridactylus*	*P. albolarvatus*	*P. villosus*	*P. pubescens*	*S. thyroides*	*S. ruber and nuchalis*	*D. pileatus*	*M. lewis*	*M. formicivorus*	*C. auratus*	Total
Pine	4	1	7	3		13	1	2	3		1	35
Lodgepole pine	4			1		4						9
Ponderosa pine		1					4		1			6
Spruce	4	9					1					14
Tamarack		4		2		6	1					13
Fir			2	4		3	4	1	1		2	17
Douglas fir				1		1						2
Mountain hemlock						5						5
Cedar	1	2										3
Juniper							3		5			10
Oak			2						9	4	1	16
Alder							3					3
Aspen	1	3	1	17	20	4	48	1			20	115
Cottonwood				4			3	2	34	3	2	48
Willow					4		2		2	1	2	11
Sycamore									2	1	1	4
Madrone				1								1
Poles	1	1		1					3	3	4	13
Total	15	21	12	33	24	36	70	6	60	12	35	325

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[1] Nest sites from outside the Northwest were included if they were in tree species which occur in the Northwest.

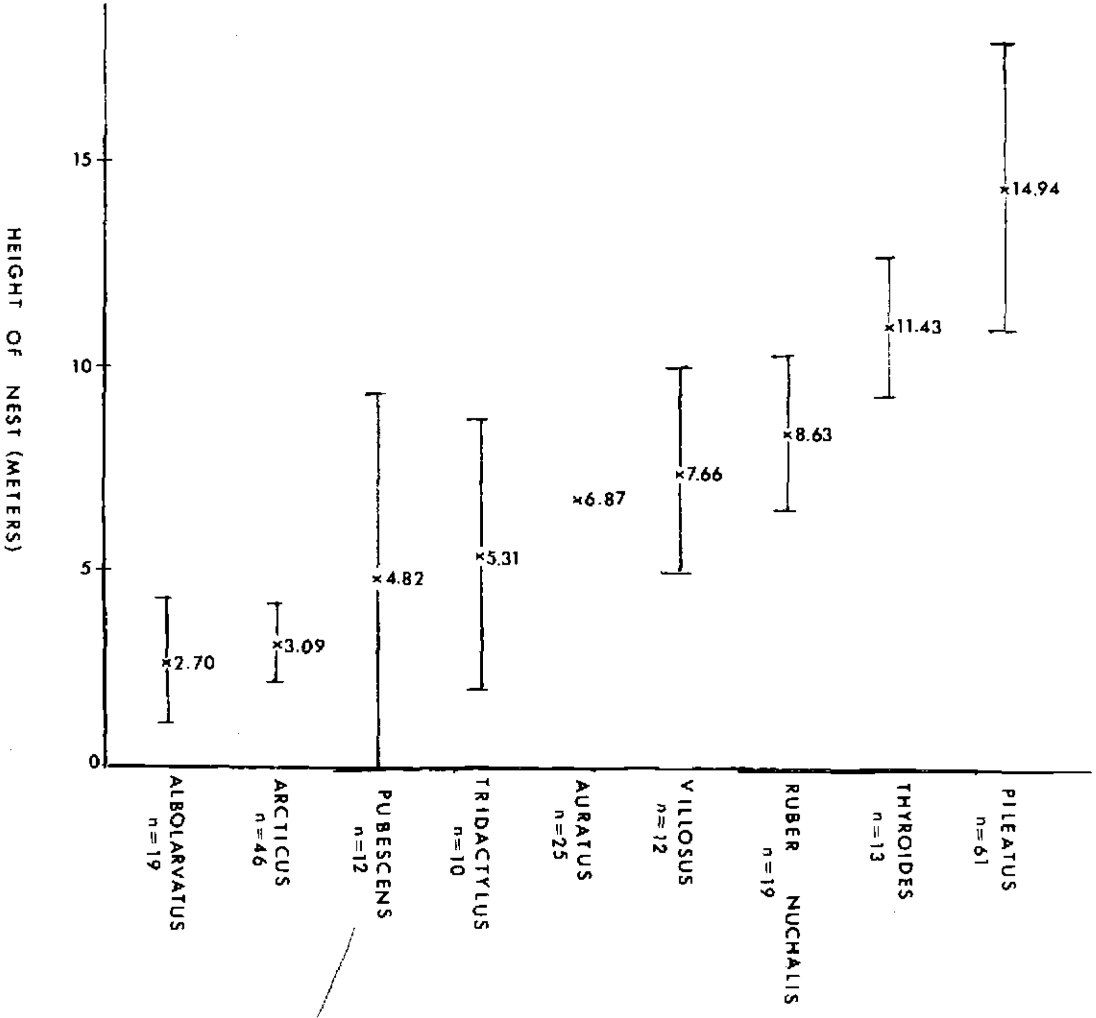

Figure 12. Average height of nest holes of woodpeckers, calculated by compiling records in the literature. Confidence intervals at p = .05. Confidence interval for <u>auratus</u> is unknown.

10 degrees below horizontal. Conner suggested that the angle of the entrance hole prevented rain from entering the cavity. Bull, studying pileated woodpeckers in Oregon, found that in trees that leaned, the hole was located on the underside of the tree (Evelyn Bull, pers. comm.).

4. Excavation of the Nest Cavity

The nesting success of woodpeckers depends greatly on close cooperation of the pair (Lawrence 1966). Excavation of the nest cavity is an important phase of the reproductive cycle in synchronizing behavior. Excavation usually takes two weeks to a month. The excavation period varies due to differences in the excavating ability of the species, hardness of the wood of the nest tree, and rhythm of the excavation behavior (Table 5).

Three stages in the process of excavation are the boring of (1) the corridor which forms the entrance part of the cavity, (2) the curved link between the corridor and the cavity, and (3) the cavity itself. Usually the outer shell of the tree is solid hard wood and the interior is softened by decay so that the initial shaping and chipping of the entrance hole requires the greatest effort.

Table 5. Length of excavation period, clutch size, length of incubation period, and length of nestling period of Northwestern woodpeckers.

	Excavation Period (days)	Common Range of Clutch Size	Incubation Period (days)	Nestling Period (days)
P. arcticus	--	4-5 (3)	--	--
P. tridactylus	--	4 (1, 3)	--	--
P. albotarvatus	--	4-7 (1, 3)	14 (2)	--
P. villosus	20 (9)	3-6 (3, 6, 9)	14 (9)	28-30 (9)
P. pubescens	16 (9)	4-5 (3)	12 (9)	20-22 (9)
D. pileatus	30 (7)	3-5 (3)	18 (7)	26 (7)
S. thyroides	--	4-6 (1)	--	--
S. ruber and *nuchalis*	20 (9)	4-7 (8)	12-13 (9)	25-29 (9)
M. formicivorus	90 (2)	4-5 (3)	--	--
M. lewis	14-21	5-9 (2)	14 (2)	28-34 (10)
C. auratus	12 (4, 9)	5-9 (3)	12 (5, 9)	26 (8)

(1) Bendire (1895); (2) Bent (1939); (3) Gabrielson and Jewett (1940); (4) Snow (1940); (t) Sherman (1952); (6) Skutch (1955); (7) Hoyt (1957); (8) Godfrey (1966); (9) Lawrence (1966); (10) Bock (1970).

5. Egg Laying

In many bird species attentiveness to the nest during the egg laying period is restricted to the laying of an egg each day. Woodpecker pairs generally spend extended periods of time near the nest hole, 40 percent of the day in downy woodpeckers and 80 percent in hairy woodpeckers (Lawrence, 1966). Attentiveness probably serves to protect the hole from would-be expropriators, and to protect the eggs from predators. Four to six eggs is the average woodpecker clutch size; lewis and auratus lay somewhat larger clutches. Woodpeckers in Oregon and Washington generally lay eggs in May (Table 5).

Incubation does not begin until all the eggs are laid. The flicker is known to be an indeterminate layer. Phillips (in Bent 1939) induced a flicker to lay 71 eggs in 73 days by removing the eggs as they were laid.

6. Incubation

Incubation lasts 11 to 14 days in North American woodpeckers with the exception of the two large species, the pileated and the ivory-billed woodpecker, whose eggs are incubated for 18 days (Table 5). Woodpeckers are in attendance at the nest almost constantly but sometimes perch outside the nest rather than actually incubating. With few exceptions (Sherman 1952) only the male incubates at night;

both sexes incubate during the day.

Lawrence (1966) found that the loss of one parent during the incubation period was fatal to the progeny. She attributed this loss to the woodpecker's inability to modify its brooding rhythm.

7. The Nestling Period

Woodpecker young are hatched naked and blind; they acquire the juvenile plumage in the nest (Hoyt 1944, Short 1963, Bent 1939). Nestlings are generally brooded constantly for the first 5 days. Thereafter brooding is intermittent during the day but young are brooded all night up until about a week before fledging. The male broods at night and both parents during the day. Feces of the nestlings are eaten by the adults for the first few days after until the adults establish the habit of carrying the feces out (Lawrence 1966).

Excavation activities within the nest hole continue throughout the nestling period (Lawrence 1966, Kilham 1962). Kilham suggested that the cavity is thereby enlarged as the nestlings grow. Lawrence suggested a secondary advantage of keeping the floor covered with dry chips and sawdust.

The nestling period of woodpeckers occurs during the time of high emergence of insects in the spring. Flycatching and surface gleaning are the primary foraging methods of most species during the nestling period (Table 6). Foraging distance from the nest varies

Table 6. Methods of foraging for a feeding of nestling woodpeckers.

	Foraging Method	Foraging Distance	Feeding Method	Feedings Per Hour
P. arcticus (2)	--	several hundred meters	direct	9.6
P. albolarvatus (1)	gleaning	400 m	--	4
P. villosus (5, 3)	gleaning	800 m	direct	10.4
P. pubescens (5, 3)	gleaning	180 m	direct	14.8
D. pileatus (4)	gleaning and ground foraging	--	regurgitation	1
S. thyroides (6)	gleaning	--	--	--
S. ruber and *nuchalis* (5)	flycatching and gleaning	--	direct	8.8
M. formicivorus (7)	flycatching	--	direct (storage)	--
M. lewis (8)	flycatching and gleaning	--	direct (storage)	15.1
C. auratus (5)	ground foraging	--	regurgitation	2.2

(1) Bent (1939); (2) England (1940); (3) Staebler (1948); (4) Hoyt (1957); (5) Lawrence (1966); (6) Stallcup (1968); (7) MacRoberts (1970); (8) Bock (1970).

between species. Both male and female feed the young.

Although most woodpeckers feed insects to the young directly, the flicker and the pileated feed by regurgitation (Hoyt 1957, Lawrence 1966). These two species forage extensively on ants. Storing up large numbers of these small insects in the stomach before returning to the nest may be more efficient than making a trip each time the bill is full. The pileated woodpecker feeds its young every one or two hours; the flicker averages 2.2 feedings per hour. The other species of woodpeckers, which feed insects directly, average ten or more feedings per hour (Table 6).

The two species which forage most extensively by flycatching, the acorn woodpecker and the lewis woodpecker, temporarily store insects before bringing them to the nest. After each capture, the bird returns to the hawking perch and pounds the insect into a crevice. This behavior is repeated several times before the insects are gathered up and carried to the nestlings (MacRoberts 1970, Bock 1970).

There are contradictory statements in the literature as to whether sapsuckers feed sap to their young. Kilham (1962a) who studied sapsuckers in New Hampshire stated that a mixture of sap and insects is brought to the nest. Foster and Tate (1966:89) wrote about their observations in Michigan

> Typically a sapsucker, on obtaining a mouthful of insects, flies to the feeding tree, where it works the insects into the wet sap and forms a bolus which it either consumes or takes to the young.

Lawrence (1966), working in Ontario, found that sap was not included in the diet of nestlings except incidentally.

Fledging occurs 3 to 5 weeks after hatching (Table 5). In most cases the young are able to sustain flight immediately upon leaving the nest hole. However Bock reported that the young of lewis woodpeckers ventured from the nest and climbed about on the trunk and limbs for two to three days before flying. Parents feed the young for a few weeks after leaving the nest (Staebler 1949, Hoyt 1957, Lawrence 1966). The family group generally remains together until the fall (Staebler 1949, Hoyt 1957, Lawrence 1966, Bock 1970). Kilham (1968) found that after fledging each hairy woodpecker parent was followed about in succeeding weeks by particular offspring which were cared for by that one parent. Bock found that adults of lewis separated and each took a part of the brood. Snow (1940) stated that female lewis alone cares for the fledglings.

Hoyt (1957) observed what appeared to be an adult pileated woodpecker teaching a fledgling to forage. Kilham (1968) reported that adult flickers taught fledglings to forage by putting food in crevices.

8. Second Broods and Renesting

With the exception of the acorn woodpecker (Ritter 1938), woodpeckers generally raise only one brood per season (Snow 1940, Hoyt 1957, Lawrence 1966, Bock 1970). Bent (1939) noted some cases of double broodedness in the southeast U.S. In Illinois, three of fifteen pairs of red-headed woodpeckers studied by Reller (1972) nested a second time, two while still feeding fledglings from the first nest. Total time from start of excavation until fledglings forage independently is shortest for downy woodpeckers (74 days), and longest for the pileated woodpecker (92 days).

Lawrence (1966) found no evidence of villosus, pubescens, varius, or auratus renesting after the first nesting was broken up except when destruction of the nest occurred at a very early stage. Conway (1957) stated that if some calamity caused the pileated to abandon its nest early in the incubation period, the birds may renest, digging an entirely new cavity. Truslow (1967) observed a pair of pileateds which renested after the first clutch was lost.

E. Winter Habits

1. Roosting

Woodpeckers almost always roost in holes (Hoyt 1957, Kilham 1959d, 1965, Lawrence 1966, Nyholm 1968) but use of a nest hole for roosting is rare (Hoyt 1957). The three-toeds, hairy, downy, and pileated woodpeckers, and the flicker are known to excavate new holes in the fall in which to roost.

Woodpeckers are tolerant of other birds close to their roost hole. Nyholm observed three birds of the same species (*Dendrocopos major*) spending the night in the same tree. Kilham (1971b) found two downy woodpeckers which excavated holes in an ash stub and roosted within a few feet of each other. He also observed a group of roost holes which were used alternately by a downy woodpecker and a white-breasted nuthatch.

2. Winter Movements

Woodpeckers are generally resident although most individuals of the species *nuchalis*, *thyroides*, and *lewis* move south in the fall. Migration is diurnal and rather slow with occasional birds straggling for a time along the way (Bock 1970).

In the autumn, after the break up of family groups, three-toed woodpeckers become nomadic, shifting about in large numbers throughout the winter (van Tyne 1926, Forbush 1927, Bent 1939, Blackford 1955, Yeager 1955, Koplin 1967). In the northeast *arcticus* and *tridactylus* populations occasionally build up to large numbers and birds migrate south in waves. This occurred in 1860 (Forbush 1927), 1924 and in 1956 (West and Speirs 1959). Van Tyne (1926) correlated the 1924 invasion with an eruption of spruce budworm in eastern Canada in 1909-1914. He reasoned that the many dead trees resulted in an increase in food supply, which led to an increase in woodpecker numbers. With the decline in insect populations in subsequent years, the birds moved south in search of food.

If the winter food supply is meager, groups of three-toeds disperse before winter is over (Baldwin 1968a). In areas of abundant food, aggregations of woodpeckers develop. Densities may become very high at foci of insect outbreaks. The largest number of woodpeckers observed by Baldwin (1960) on his study area in Colorado was 60 to 90 individuals drifting through and continually being replaced by new individuals (Baldwin 1960). Each night almost all of the woodpeckers in Baldwin's study area moved away, up to .8 km to roost. There were at least 90 cavities on his study area of 54 hectares but most of them were not used by roosting woodpeckers.

During the day feeding groups would often act in a somewhat coordinated manner. Frequently groups would move or filter along such that the whole group would be encountered elsewhere in the grove 1/2 hour later. Antagonism between members of the same species was noticeable, however when feeding avidly, often 4-6 individuals of one or more species would feed peacefully as close together as 30 cm on the same trunk (Baldwin 1960).

The white-headed woodpecker is a resident species, becoming somewhat nomadic during the winter, and foraging primarily on pine seeds (Beal 1911, Wetmore 1964, Ligon 1973). These birds sometimes form small flocks of 4 to 6 (perhaps family groups) and move through the forest concentrating in areas with large cone crops. Albolarvatus is an important predator of pine beetles during outbreaks (Otvos 1965). They usually feed in pairs and will move into an infestation after the bark is partly peeled off by hairy woodpeckers.

Hairy woodpeckers are resident and forage extensively on seeds. They flock with chickadees and kinglets in winter (Bent 1939, Morse 1970). Hairys aggregate in areas of insect epidemics (Koplin 1967).

Pubescens is a resident species, showing less tendency to wander than the three-toeds or the hairy although its numbers do increase during insect outbreaks (Koplin 1967). Pubescens tends to remain in the vicinity of a roost hole throughout the winter (Bent 1939). Downy woodpeckers often use bird feeders in winter (pers. obs.).

Of the sapsuckers, nuchalis and thyroides are migratory and ruber is resident. Nuchalis and thyroides winter in southwestern United States and northwestern Mexico including Baja California (Howell 1952). The birds migrate from the beginning of September through October and return in the spring around the last week of March (Gabrielson and Jewett 1940). During the winter, ruber is dependent to some degree on the cambium and sap of coniferous trees because deciduous trees are dormant. Ziller and Stirling (1961) postulated that large numbers of sapsuckers perish during severe winters when the sap of coniferous trees freezes.

Pileated woodpeckers are resident but are reported to wander extensively in winter (Beal 1911, Evelyn B~~a~~ull, pers. comm.).

Lewis woodpeckers winter where there are oaks and where the weather is mild enough for some emergent insects to be available (Bock 1970). Most individuals breeding in Oregon and Washington migrate to California early in fall, wintering in oak woodlands and commercial orchards, however many birds which breed in the Willamette Valley and along both sides of the Columbia River from around Prescott to The Dalles remain resident year round. Throughout this area of permanent residence, groves of *Quercus garryana* are present (Franklin and Dyrness 1973), and provide *lewis* with mast for winter storage (pers. obs.). In Oregon, winter residents are most abundant in the Rogue and Umpque River regions. Bock (1970) pointed out that in southern Oregon a variety of oaks reach the northern limit of their distribution and suggested that the high diversity of oak species insured a more regular acorn supply.

Migratory routes of this species are not fixed because *lewis* is highly opportunistic, nesting where insects are temporarily abundant and, in winter, concentrating in areas with good crops of acorns.

Migration begins in late August and continues into September. They arrive back on the breeding ground in late April or early May. Bock (1970) estimated that an average of 13 days was spent migrating in the spring and about 23 days in the fall. Migration is longer in the fall because lewis woodpeckers generally do not travel directly from breeding grounds to wintering grounds but in late summer form nomadic flocks, of up to 300 or more birds (Bent 1939). These nomadic flocks move into the higher mountains or invade orchards in search of fruit. These flocks may do considerable damage to fruit crops (Neff 1926).

Acorn woodpeckers are highly sedentary. They remain with their colony and their acorn stores all year around.

Flickers are resident birds. In winter they are most often seen in flocks foraging in fields or other open places and often with robins. There is some vertical migration from higher elevations to valleys.

IV. ROLE OF WOODPECKERS IN THE FOREST

A. Introduction

The role of woodpeckers may be defined as the part they play in the complex of interactions of organisms in their community. Two topics will be discussed in detail. The most significant role of woodpeckers in the forest is probably providing nest holes for other species. Cavity nesting is a highly successful strategy among birds. Cavity nesting birds have adapted to common problems in similar ways. In the Northwest, woodpeckers along with chickadees and nuthatches are capable of excavating a nest hole. Other cavity nesters must rely on natural holes or those drilled by excavators in previous years.

Woodpeckers also play a role as the primary predators of many bark and wood boring insects. Their impact is often great enough to prevent insect outbreaks.

B. The Cavity Nesters

1. Introduction

Nests may be categorized as open (characteristic of about 70 percent of all bird species), domed (5 to 10 percent of bird species), crevice (5 percent of bird species) and hole nests (15 to 20 percent of bird species) (von Haartman 1957). Holes in the ground are here called burrow nests and holes in trees cavity nests. Table 7 is a list of all cavity nesting species breeding in Washington and Oregon. Eighteen of the 43 species of cavity nesters in Oregon and Washington are excavators. Nuthatches and chickadees excavate small holes with an entrance about 3 cm in diameter. They sometimes excavate in the thick, soft bark of douglas fir (Erskine and McLaren 1972). Woodpecker holes vary from 3 to 11 cm in diameter. There are 17 species of cavity nesting birds which almost always nest in holes but do not excavate them, and nine species which sometimes nest in holes but also nest in other places.

2. Density of Cavity Nesting Pairs

The Annual Breeding Bird Census published in American Birds was used as a source of data on populations of cavity nesters in the Northwest. These censuses, some of which have been taken every spring for about 20 years, are conducted on study areas of about 8 hectares. Vegetation descriptions of the areas are prepared, along with pertinent geographical facts, weather conditions, etc. The breeding birds are censused by sight, usually each morning for about a week; the total time for each area censused averages about 24 hours. Average number of pairs of each species per 40 hectares is calculated and the results are published.

Table 7. Avian cavity nesters which breed in Oregon and Washington.

Excavators

- red-breasted nuthatch (*Sitta canadensis*)
- white-breasted nuthatch (*Sitta carolinensis*)
- pygmy nuthatch (*Sitta pygmea*)
- black-backed three-toed woodpecker
- northern three-toed woodpecker
- white-headed woodpecker
- hairy woodpecker
- downy woodpecker
- pileated woodpecker
- red-breasted sapsucker
- red-naped sapsucker
- williamson's sapsucker
- acorn woodpecker
- lewis woodpecker
- common flicker
- black-capped chickadee (*Parus atricapillus*)
- mountain chickadee (*Parus gambeli*)
- chestnut-backed chickadee (*Parus rufescens*)

Nest in Cavities

- wood duck (*Aix sponsa*)
- common goldeneye (*Bucephala clangula*)
- barrow's goldeneye (*Bucephala islandica*)
- bufflehead (*Bucephala albeola*)
- harlequin duck (*Histrionicus histrionicus*)
- hooded merganser (*Lophodytes cucullatus*)
- spotted owl (*Strix occidentalis*)
- sawhet owl (*Aegolius acadicus*)
- screech owl (*Otus asio*)
- pygmy owl (*Golaucidium gnoma*)
- flammulated owl (*Otus flammeolus*)
- sparrow hawk (*Falco sparverius*)
- tree swallow (*Iridoprocne bicolor*)
- purple martin (*Progne subis*)
- western bluebird (*Sialia mexicana*)
- mountain bluebird (*Sialia currucoides*)

Sometimes Nest in Cavities

- common merganser (*Mergus merganser*)
- barn owl (*Tyto alba*)
- starling (*Sturnis vulgaris*)
- house sparrow (*Passer domesticus*)
- violet-green swallow (*Tachycineta thalassina*)
- house wren (*Troglodytes aedon*)
- winter wren (*Troglodytes troglodytes*)
- bewick's wren (*Thryomanes bewickii*)
- house finch (*Carpodacus mexicanus*)

All censuses which were made in habitats which occur in Oregon and in which cavity nesting species were found were included in the sample. Thus if a census of old growth douglas fir was conducted in California, I recorded it. This resulted in a sample of 63 censuses. Overall 0.26 ± 0.08 ($p = 0.05$) of the total bird pairs were cavity nesters for an average of 74 ± 19 cavity nestling pairs per 40 hectares of a total breeding bird density of 300 ± 65 pairs per 40 hectares.

No significant differences in proportion of cavity nesters in habitats classified by tree species were found (probably because sample sizes were too small) (Figure 13). The largest proportion of cavity nesting pairs was found in ponderosa pine (0.33 ± 0.16) and oak (0.34 ± 0.11). Cavity nesting pairs comprised the least proportion in spruce fir (0.17 ± 0.13), and douglas fir (0.14 ± 0.04). I found a significant difference between the proportion of cavity nesting pairs in deciduous (0.28 ± 0.02), coniferous (0.21 ± 0.02), and mixed forest (0.38 ± 0.04). Many of the mixed species forest may have been transitional stages between an earlier deciduous and later coniferous stage. Hardwoods dying out under the coniferous canopy make good nest trees and thus increase the density of hole nesting pairs. Haapanen (1965) found an increase in cavity nesting pairs from 10 to 42 pairs/40 hectares in a spruce forest during the transitional stage when early successional trees are dying and being supplanted by later succession species.

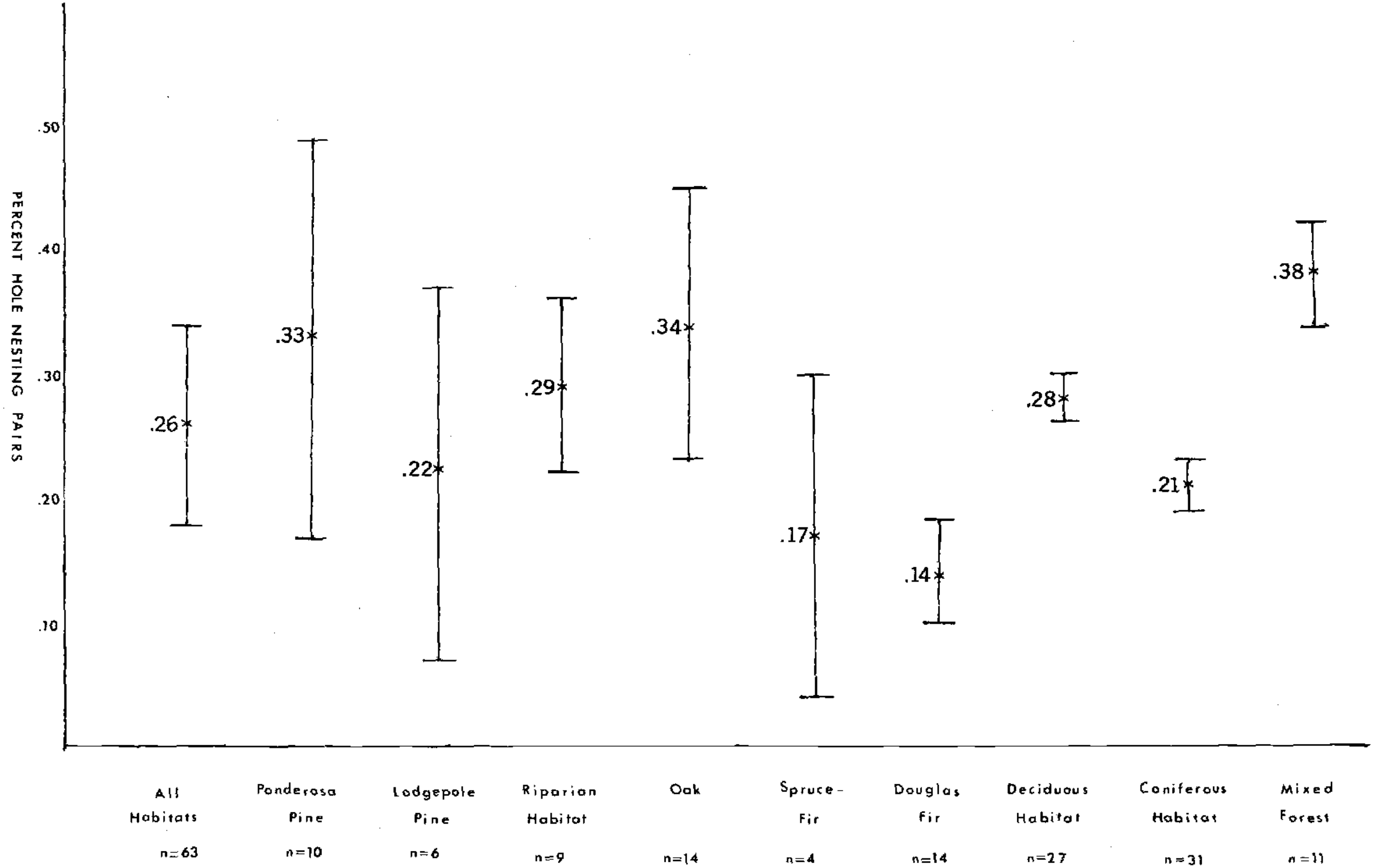

Figure 13. Percent of breeding pairs which nest in cavities in deciduous, coniferous, and mixed forests and in habitats classified by dominant tree. Points plotted are means surrounded by .05 confidence intervals. Calculated from data from the Annual Breeding Bird Censuses, 1947-73, reported in <u>American Birds</u>.

3. Nesting Success

Bird nests provide a place to lay the eggs and raise the young. They afford escape from predators either by camouflage or inaccessibility, and protection against inclement weather particularly cold. Cavities are superior to other nest types in several ways. The wooden walls of the cavity provide excellent insulation retaining the body heat of the incubating or brooding parent and later the body heat of the nestling (Kendeigh 1961, Royama 1966). The nestlings are almost completely protected from rain, wind or strong sun. Protection from predators is probably mainly by inaccessibility. Camouflage is probably a minor part of the cavity nesting strategy. Although the cavity may hide the young from some predators, the round dark hole is evident to many predators such as squirrels, raccoons and jays.

Predation is probably the one factor most responsible for reproductive failure in birds. In a study of birds nesting in deciduous scrub, Nolan (1963) found that 88 percent of all nest failures were due to predation. Cody (1971) cited predation as the single greatest cause of reproductive failure in most species of birds. He suggested that it is this factor rather than food abundance which most often operates in a density dependent fashion to regulate population density.

The superiority of cavity nests over other nest types has been confirmed by studies of fledging success. Nice (1957) found that cavity nesting passerines had a fledging success of 66 percent, while open nesters had a fledging success of 46 percent. Similarly Kalmbach (1939) estimated a hatching success of 73 percent for North American cavity nesters excluding ducks, 43 percent for ground nesters, and 52 percent for bush and tree nesters.

4. Availability of Nest Cavities

There is evidence that the density of cavity nesting pairs is limited primarily by the number of available holes. This was demonstrated in a German forest in 1917; resource managers successfully increased populations of cavity nesters by providing nest boxes (Wolda 1917). More recently, Pfeifer (1963) working in Germany, has achieved astounding increases in the density of cavity nesters by providing nest boxes. In the smaller of his two study areas (1.25 ha.) the number of successfully fledged broods was increased from zero to 29.66 and in a larger study area (25 ha.) from 1.7 to 25.7. These figures are average increases over a nine year period.

Further evidence that a limiting factor for cavity nesters is cavities comes from a study of forest birds in Finland (Haapanen 1965) (Table 8). He compared the density of cavity nesters and open nesters in managed and unmanaged forests. In the managed forests he studied, no snags were left, deciduous trees were removed, and the stands were periodically thinned. In every case he found significantly fewer cavity nesting pairs in the managed forest while the density of birds nesting in the open was approximately the same. In pine forests there were no fewer open nesters but 44 percent fewer cavity nesting pairs. Similarly in the spruce forests there were five percent fewer open nesters and 68 percent fewer cavity nesters. The decrease in cavity nesters is almost certainly due to a decrease in the number of available nest sites in managed forests.

Table 8. Density of birds (pairs/KM^2) found in managed as compared to natural forests in Finland (Haapanen 1965).

	Open Nesters	Cavity Nesters
Pine Forest		
Natural	91	39
Managed	91	22
	(0% decrease)	(44% decrease)
Spruce Forest		
Natural	149	59
Managed	142	20
	(5% decrease)	(68% decrease)

Further evidence that cavity nesters are primarily limited by nest sites was given by MacKenzie 1952, Herberg 1953, 1960, Creutz 1955, Campbell 1955, Bruns 1960, and Hammerstrom et al. 1973.

5. Sources of Nest Cavities

Other than nest boxes there are two sources of nest cavities, those that develop through wood decay and those drilled by excavators, mainly woodpeckers. The latter are probably much preferred to natural holes because of the shape of the cavity and the size of the entrance hole. Natural cavities tend to be shallow and have large entrance holes which may make their inhabitants more exposed to predators. The supply of cavities formed by wood decay is probably quite limited. In Finland Haapanen (1965) found that although the density of hole nesters varied greatly with the habitat, the ratio of excavating pairs to non-excavating pairs remained at about 1:2. The number of non-excavating pairs present was correlated with the number of excavators present which implies that the non-excavators rely on the excavators to provide them with holes.

The fact that holes are in short supply gives rise to the question why don't more birds excavate holes? The answer undoubtably lies in the fact that very specialized morphological adaptations are required to enable a bird to deliver the heavy blows necessary to excavate. These adaptations such as a shock absorbing mechanism, heavy chisel shaped bill, and trunk climbing posture are only developed at the expense of morphological features which are not expendable in most species.

6. Cavity Nesting as a Breeding Strategy

Lack (1968) demonstrated that cavity nesting birds tend to have prolonged nestling periods. The average nestling period for European passerines nesting in cavities is 17.3 days. Birds using open nests average 13.2 days. Woodpeckers average about 26 days. Cavity nesters also tend to have large clutches. Lack (1968) found a correlation between nestling period and clutch size. He suggested that the slowed growth rate of nestlings permits the parents to raise a larger clutch because each offspring needs to be provided with less food per unit time. Because of the insulation the hole provides, the parents need to spend less time brooding the young (Royama 1966), and therefore have more time to devote to feeding. These arguments assume that food is the factor limiting clutch size in birds. If food abundance were a limiting factor one would expect high densities of breeding pairs to have a lower reproductive success than low densities. Tompa (1967) found no decrease in fledging success of pied flycatchers with an increase in breeding density from 1/4 to 20 pairs per hectare.

The longer nestling period of hole nesters may be an adaptation to reduce loss by predation. There is selection for fast growth of the nestlings of open nesting birds because high nest predation makes it important for the young to get out of the nest as quickly as possible. The young in cavity nests are probably safer in the nest than out.

Von Haartman (1954b) found that the period of weight increase in the young of hole nesters is only moderately prolonged. The prolongation of nestling time is due primarily to the time elapsing between the young's reaching full weight and leaving the nest.

Many birds particularly passerines raise more than one clutch per season. Hole nesters characteristically do not. The hole is used once and then abandoned; it is not even used for roosting. Possibly the habit of nesting once and then abandoning the hole is due to the influence of nest parasites. Build up of ectoparasites during the first nesting may make attempting to raise a second clutch unprofitable. The studies of Rothschild and Clay (1952) demonstrated that nests which are built in holes, and which are returned to year after year contain on an average a larger number of individual parasites and a greater variety of species than other nests. Bird house owners are aware of the importance of cleaning out the houses thoroughly before the birds arrive to breed in the spring.

If ectoparatistes are an important factor in preventing renesting in hole nesters, the characteristically larger clutch sizes of these species may be a strategy to circumvent this limitation; i.e., it is more profitable to raise one large clutch than to raise two small ones.

Many ectoparatsites overwinter in the nest (Rothschild and Clay 1952). This factor may have contributed to the woodpecker's habit of excavating a new hole every year. Some ectoparasites particularly

Mallophaga are highly host specific (Rothschild and Clay 1952). Thus a non-excavator using an old woodpecker hole is not subject to as great an infestation as the original excavator would be on second use. Ectoparasites such as fleas (Siphonaptera) and louse flies (Hippoboscidae) are generalized in host preference being parasitic on a group of birds with similar nesting habits which provide the preferred microclime.

7. The Relation Between Winter Residency, Roosting in Cavities, and Early Breeding

Von Haartman (1968) has collected some data from Finland and Ontario (Table 9) which demonstrate that cavity nesting birds tend to be resident rather than migratory. In both places 50 percent of the cavity nesting species were resident whereas only about 10 percent of the non-cavity nesters were resident. Von Haartman's data on Finnish passerines suggests that there is also a trend toward early breeding in cavity nesters. Both these trends may relate to a shortage of nest holes: the most reliable way to secure a hole or a good excavation site is to be resident and to breed early.

Cavity nesting species characteristically roost overnight in holes during the winter. Roosting in holes reduces winter mortality and may allow a species to occur farther north than it otherwise would. Kendeigh (1961) demonstrated that the air inside a roosting cavity is

Table 9. Migratory status of cavity nesters compared to other birds in Finland and Ontario (von Haartman 1968).

	Finland				Ontario			
	Cavity Nesters		Others		Cavity Nesters		Others	
	Number of Birds	Percent	Number of Birds	Percent	Number of Birds	Percent	Number of Birds	Percent
Resident	9	.50	11	.15	9	.50	11	.09
Partial migrant	1	.06	6	.08	1	.06	3	.03
Mainly migrant	1	.06	3	.04	0	0	17	.15
Migrant	7	.39	53	.73	8	.42	83	.73
Total	18		73		18		114	

maintained at a fairly constant temperature throughout the night even though the temperature outside drops (Figure 14). His study of a house sparrow in Illinois showed that on an average night when the outside temperature dropped from 5° C at 4:00 pm to -1° C at 7:00 am the temperature inside the nest box remained between 4-1/2 and 8-1/2° C all night. Kendeigh suggests that the amount of energy conserved may make the difference between survival and death during periods of extreme cold. At -8° C a bird which roosts in a cavity conserved 1.86 kcal per night over a bird which roosts in the outside air. This is 11.1% of the total energy required for roosting (i.e., to maintain body temperature from 4:00 pm to 7:00 am).

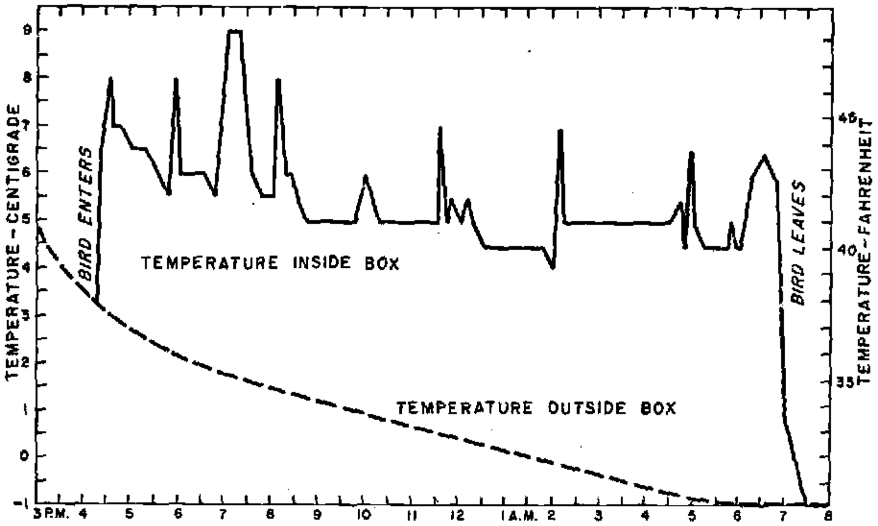

Figure 14. Temperature inside and outside the nest box of a house wren on an average night (Kendeigh 1961).

8. Nest Hole Competition

Competition among cavity nesters for nest sites if often strong. Severe fighting for the nest hole occurs. Von Haartman (1956) watched two pied flycatchers fight to the death over a nest hole.

McLaren (1963) studied 20 cavity nesting species inhabiting a douglas fir forest in British Columbia. These species fell into three natural groups on the basis of hole size. The group dependent on holes made by the flicker showed evidence of nest site competition. Birds nesting in small holes were mainly excavators; too little data was collected on birds dependent on holes of the pileated woodpecker, to draw any conclusions. McLaren suggested that competition may have been absent from the medium hole group before the advent of the starling, which occupies about 25 percent of the medium-sized holes. Table 10 is an attempt to group the 43 species of cavity nesters found in Oregon and Washington.

Use of abandoned woodpecker holes by cavity nesters is not a direct detriment to the woodpeckers. However, the more aggressive cavity nesting species will expropriate newly excavated woodpecker holes which are in use.

The habit of excavating a new hole every year may have been selected for because it reduces conflict with other cavity nesting species. Over the years those individuals that relinquished the old

Table 10. Grouping of non-excavating cavity nesters with the excavators of similar size. (Total lengths are from Robbins et al., 1966).

Excavators	Non-Excavators
Small birds (8 3/4-17 1/2 cm total length)	
white-breasted nuthatch	bewick's wren
red-breasted nuthatch	winter wren
pygmy nuthatch	house wren
black-capped chickadee	tree swallow
mountain chickadee	violet-green swallow
chestnut-backed chickadee	western bluebird
downy woodpecker	house sparrow
	house finch
Medium birds (18 3/4-20 cm total length)	
black-backed three-toed woodpecker	mountain bluebird
northern three-toed woodpecker	ash-throated flycatcher
white-headed woodpecker	starling
hairy woodpecker	purple martin
red-breasted sapsucker	sawhet owl
red-naped sapsucker	flammulated owl
acorn woodpecker	pygmy owl
Large birds (21-37 1/2 cm total length)	
pileated woodpecker	screech owl
williamson's sapsucker	spotted owl
lewis woodpecker	barn owl
common flicker	sparrow hawk
	wood duck
	common goldeneye
	barrow's goldeneye
	harlequin duck
	hooded merganser
	common merganser

hole and dug a new one were more successful than those individuals who fought over the hole with the resident pair. Conflict over nest holes has almost certainly had a strong influence on the life history of cavity nesters.

A variety of species have been observed to appropriate woodpecker holes. Bent (1939) described an incident in which a red squirrel (Tamiasciurus hudsonicus) ate a hairy woodpecker's eggs and then moved its young into the vacated hole. Bent quoted Gault as stating that in Illinois the hairy woodpecker was becoming a rare breeder owing to the fact that the English sparrow appropriated almost every nest hole as soon as it was excavated. English sparrows will remove newly hatched woodpecker young from the nest and throw them on the ground. Wilson (1832 from Bent) saw a pair of downys driven from their nest by house wrens. Kilham (1959d) observed a wood duck taking over the nest of a pileated woodpecker.

The frequency of aggressive interactions may be quite high. In 177.9 hours of observations during the breeding season Bock (1970) observed 115 aggressive interactions involving the lewis woodpecker. Frequent interactors were sparrow hawk (21), plain titmouse (18), starling (14), acorn woodpecker (12), white-breasted nuthatch (8), flicker (7). All of these species are cavity nesters.

Woodpeckers are generally successful in defending their nest hole against aggressors (Lawrence 1966), however frequent bouts with intruders will disrupt the normal breeding behavior. Lawrence (1966:131) wrote of two downy woodpeckers involved in a series of conflicts with a red squirrel:

> From being kept in this prolonged state of ultra-high tension the downy woodpeckers were led to react in an increasingly confused and contradictory manner. This took expression in a series of displacement and redirected activities which persisted long after the squirrel incident had come to an end.

C. Response of Woodpeckers to Insect Outbreaks

1. Introduction

Densities of forest insects fluctuate irregularly and dramatically. Some insectivorous birds, called irruptive species (Morse 1971), are adapted to respond both functionally and numerically to localized superabundances of prey. Woodpeckers which winter in northern forests fall into this category. Their response to epidemics of engelmann spruce beetles has been well documented and forms the basis for this discussion. Densities of northern three-toed, hairy and downy woodpeckers may increase as much as 85 fold in such outbreaks (Koplin 1969, Baldwin 1960).

2, Outbreaks of Engelmann Spruce Beetles

During the summer engelmann spruce beetles excavate an egg gallery in the phloem of the mainstem of a tree. Shortly afterwards the eggs hatch and small larvae mine outward. The pupae develop in cells close to the bark surface. The emergent adult beetles attain a length of approximately 7 millimeters. In warm environments, the life cycle may be completed within one year; however, in much of the spruce-fir forests of Colorado, a two year cycle predominates.

Koplin (1972) characterized insect abundances as endemic, epidemic, and pan-epidemic (Table 11). At endemic levels of engelmann spruce beetles green trees are generally not attacked; wind thrown trees are the major source of mature beetles that perpetuate local populations (Massey and Wygant 1954, Shook and Baldwin 1970, McCambridge and Knight 1972, Koplin and Baldwin 1970).

Table 11. Number of beetles per hectare and infected trees per hectare, and area of the outbreak (hectares) under endemic, epidemic, and pan-epidemic population conditions of engelmann spruce beetles (Koplin 1972).

	Endemic	Epidemic	Pan-epidemic
Beetles/hectare	< 25[1]	25-125[1]	> 125[3]
Infected trees/hectare	2500[2]	400,000[2]	4 million[2]
Area of outbreak (hectares)	--	.4-10[1]	> 20[3]

[1] P. H. Baldwin, unpublished data from Koplin (1972).

[2] Koplin (1967).

[3] Hutchison (1951).

In pan-epidemics the density of insects in the bark of live trees may be as high as 1,000 hibernating beetles/meter^2 with an average of 250-600/meter^2. A single tree may contain 8,000 to 10,000 larvae and adults (Massey and Wygant 1954).

Koplin (1972) formulated a deterministic model which predicts the predatory impact of tridactylus, villosus, and pubescens on endemic, epidemic, and pan-epidemic populations of larval spruce beetles. The model incorporates data on food requirements of woodpeckers, average number of prey per stomach, population density of wood-peckers and air temperature as inputs. The prediction is the number of prey consumed per acre-year. The results of this model are in very close agreement with field estimates of predatory impact arrived at by several workers (Table 12).

The total response of woodpecker populations to outbreaks is to consume more beetles. This response can be broken down into a numerical and a functional component, both of which vary with the species of woodpecker.

An increase in the density of individual predators occurs initially through aggregation of birds from surrounding areas. Northern three-toeds exhibit the strongest numerical response to engelmann spruce beetles, increasing from 1 to 2 birds per 40 hectares in endemic areas (Koplin 1969), to 25 to 45 in epidemic (Amman 1958, Amman and Baldwin 1960, Baldwin 1960), and to 68 birds per 40 hectares in a pan-epidemic outbreak (Hutchison 1951). Villosus and pubescens exhibit similar but less dramatic increases in

Table 12. Summary of studies of the responses of woodpeckers to insect outbreaks in western coniferous forests.

	Woodpecker Density (per hectare)	Insect Density (per hectare)	Predatory Impact (percent reduction)	Season	Location	Investigator
Engelmann Spruce Beetle	--	1,000-2,500	0.48	winter	Colorado	Shook and Baldwin (1970)
(*Dendroctonus obesus*)	--	1,000-2,500	0.71	summer	Colorado	Shook and Baldwin (1970)
	0.25-1.0	2,500	0.13	year	Colorado	Koplin and Baldwin (1970)
	0.25-1.0	2,500	0.25	year	Colorado	Koplin and Baldwin (1970)
	2.5-3.5	4 million	0.55	--	Colorado	Hutchison (1951)
	--	4 million	0.45-0.98	year	Colorado	Knight (1958)
	0.05-.08	1,000-2,500	0.20-0.50	year	Colorado	Koplin (1967)
	3.4	400,000	0.84	year	Colorado	Koplin (1967)
	3.1	400,000	0.59	year	Colorado	Koplin (1967)
	--	400,000	0.70-0.79	--	Colorado	Baldwin (1968b)
	3.4	400,000	--	winter	Colorado	Baldwin (1968a)
	0.8	400,000	--	summer	Colorado	Baldwin (1968a)
	--	4 million	0.44-0.98	--	Colorado	Massey and Wygant (1954)
Western Pine Beetle (*Dendroctonus brevicomis*)	0.5	moderately large	0.32	year	California	Otvos (1965)
Dendroctonus rufipennis	3.0	epidemic	0.49	Oct-May	Colorado	McCambridge and Knigh (1972)
	4.5	epidemic	0.24	Oct-May	Colorado	McCambridge and Knigh (1972)
Ips pilifrons	--	--	0.65	winter	Colorado	Shook and Baldwin (1970)
	1.5	high epidemic	--	June-Dec	Colorado	Koplin (1969)
Unknown (insect increase	8	--	--	Nov	Montana	Blackford (1955)
following fire)	23	pan epidemic	--	Sept	Colorado	Yeager (1955)

density (Table 13).

Table 13. Abundances of woodpeckers in forests supporting different population levels of spruce beetles (Koplin 1972).

	Number of Woodpeckers per 40 Hectares		
	Endemic[1] Populations	Epidemic[2] Populations	Pan-epidemic[3] Populations
P. pubescens	0	4-45	32
P. tridactylus	1-2	25-45	68
P. villosus	0-2	11-57	26

[1] Koplin (1969).

[2] Amman (1958), Amman and Baldwin (1960), Baldwin (1960).

[3] Hutchison (1951), Yeager (1955).

The numerical response of woodpeckers is not proportional to the increase in prey density at high prey densities. There may be a maximum numerical response to insect outbreaks which is determined by the density of woodpeckers in the surrounding non-infested countryside. The radius from which individuals are drawn to an outbreak is not known. In extended epidemics numerical increase may come about through increased reproduction. On a western pine beetle infestation Otvos (1965) found that trees killed by beetles added to the availability of nesting sites. Breeding densities of tridactylus at an engelmann spruce beetle pan-epidemic were increased 6 to 7 fold (Baldwin 1960). Koplin (1972) suggested that territoriality ultimately limits the numerical response of northern three-toeds to increasing prey density.

Neither hairy or downy woodpeckers nest in engelmann spruce forests. Both descend to lower elevations during the breeding season (Baldwin 1960). Their reproductive response to insect epidemics is probably minimal because each species is subject to its "normal" limitations during the breeding season regardless of the state of the engelmann spruce beetle population.

The functional response of a predator to prey density is defined by Koplin (1972) as the change in the total number of a prey species consumed per predator with change in the density of the prey species. Predators often concentrate on the prey species which is most abundant. Tridactylus, villosus, and pubescens respond in this way to a super abundance of engelmann spruce beetles. The functional response of tridactylus is the greatest except during the pan-epidemic infestation (Table 14). In a pan-epidemic, spruce beetles are the only prey taken and consequently functional response is limited by stomach capacity. (The digestive rate is approximately the same in closely related species eating similar food (Koplin 1972).) Because the hairy woodpecker, has the largest stomach, it exhibited the greatest maximum functional response.

At lower insect densities the foraging adaptations of the three species are an important factor determining functional response. The northern three-toed foraged on recently dead engelmann spruce trees, and therefore encountered the greatest proportion of engelmann spruce beetles. The hairy woodpecker foraged on all tree species rather indiscriminately and so encountered a lesser proportion of the spruce beetle. The downy woodpecker, foraging mainly on twigs, encountered even less (Koplin 1967). The analyses of stomach contents of these species confirm the behavioral observations (Table 14).

Table 14. Number of prey in stomachs of woodpeckers collected in forests supporting different population levels of spruce beetles (Koplin 1972).

	Endemic	Epidemic	Pan-epidemic[1]
P. pubescens	--	3 (n=16)	36
P. tridactylus	2 (n=24)	11 (n=88)	52 (n=77)
P. villosus	0.3 (n=18)	7 (n=21)	59

[1] Numbers of prey during pan-epidemic are maximum stomach capacities.

3. Predatory Impact of Woodpeckers

The practical question is how effective are woodpeckers in controlling insect outbreaks? The results of Koplin's (1972) model, summarized in Figure 15, predict that there is an optimal prey density at which the combined functional and numerical responses of the woodpeckers are most limiting to the prey population. This occurs at engelmann spruce bettle densities of about 375,000 per hectare (epidemic level); the model predicts that 84 percent of an epidemic beetle population will be consumed.

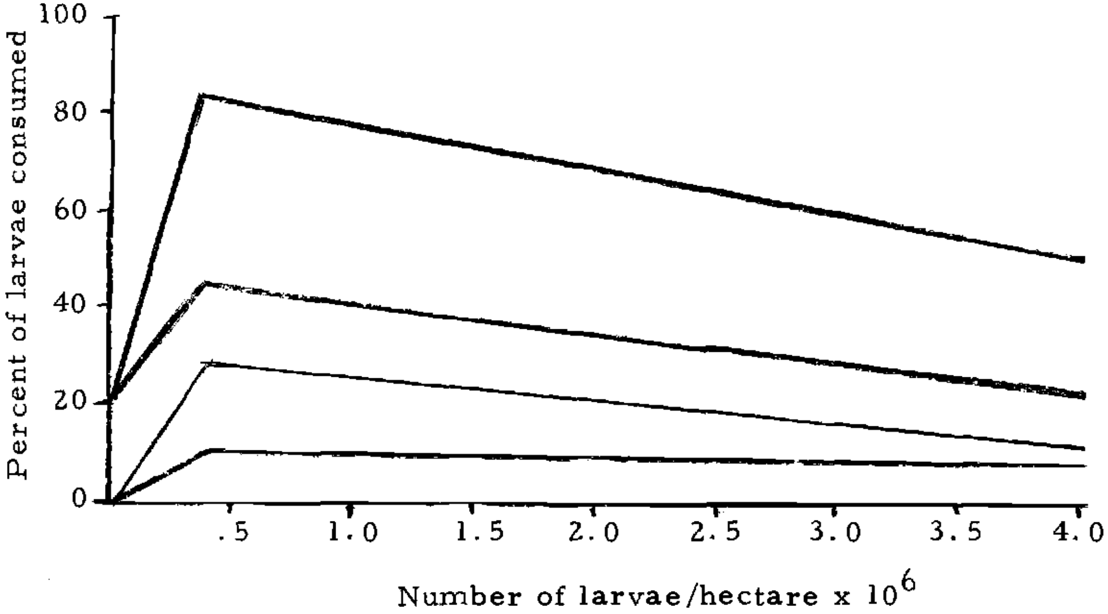

Figure 15. Predicted impact of woodpeckers on larval spruce beetles at insect densities of zero to 4 million beetles per hectare (Koplin 1972).

Woodpeckers have been shown to depress forest insect populations indirectly as well as by predation. Otvos (1965) divided the effects of predation by woodpeckers on western pine beetles into a direct reduction through actual consumption and indirect reduction through increased mortality owing to some modification of the environment. Actual consumption led to a 31.8 percent decrease, however parasitism was increased by a factor of 3.85 where woodpeckers had foraged. He attributed this increase to removal of bark by the woodpeckers which allowed a greater success of parasites with short ovipositors such as Cecidostiba sp. and Raptrocerus sp. Larval dessication resulting from bark removal by woodpecker feeding on engelmann spruce beetles is discussed by McCambridge and Knight (1972) and by Massey and Wygant (1954) as an additional source of mortality.

Field estimates of the percent of engelmann spruce beetle larvae which are consumed by woodpeckers under a range of conditions (Table 12) are in general agreement with the predictions of Koplin's model (Table 15). The model predicts that 20 percent of an endemic population, 84 percent of an epidemic, and 59 percent of a pan-epidemic population are consumed. Thus a very dense population of beetles can swamp out the pressure of woodpecker predation. Localized outbreaks are probably effectively controlled by woodpeckers. Field evidence for this conclusion is the occurrence throughout subalpine forests of small groups of spruce trees killed by spruce beetles which in turn have been destroyed by woodpeckers (N.G. Wygant, pers. comm. to J.F. Koplin 1972).

Table 15. Comparison of observed and predatory impact of woodpeckers on spruce beetles with values predicted by Koplin's (1972) model.

	Endemic	Strong Epidemic	Pan-epidemic
Number of beetles eaten by woodpeckers per hectare - year			
Predicted:			
P. pubescens	0	49,250	387,250
P. tridactylus	400	178,000	1,165,250
P. villosus	50	110,000	535,750
Total	450	338,250	2,098,250
Observed Total:	475	343,000	2,252,500

V. WOODPECKERS AND WOOD DECAYING FUNGI

A tree to be excavated, whether living or dead, must have undergone a degree of wood rot, which softens the wood (Lawrence 1966). Possibly the pileated and three-toed woodpeckers are capable of drilling in sound wood, but woodpecker holes are found almost exclusively in wood that has undergone some decay. Holes may be found in standing dead trees, in dead limbs of live trees, or in live trees with rotted heartwood. An optimum nest site is one in which the limb or trunk retains a hard outer shell protecting the nestlings from predators (Kilham 1971a).

Wood decay comes about through the action of fungi. Fungi have a limited capacity to grow in living tissue (Smith 1970). On live trees only those spores which come in contact with exposed heartwood can initiate infection. Direct contact is typically provided by wounds of various kinds such as dead or broken branches, fire wounds, and bird and insect borings (Meinecke 1929). Woodpeckers through their foraging and excavating create many openings for fungal invasion (Everett Hanson, pers. comm.).

Wood decaying fungi exhibit variable rates of growth; extremes range from .01 to 15 feet per year (Smith 1970). In general there is a positive correlation between the amount of wood decay and the age of the tree. Thus young trees offer few potential excavation sites to woodpeckers. Different tree species exhibit different resistances to fungal attack (Table 16). Aspen is very susceptible and is frequently used by woodpeckers for nesting (Table 5). Erskine and McLaren (1972) working in British Columbia found that in their study area virtually all aspens of diameter greater than 20 cm were rotted in the heartwood and most trees of this size contained one or more woodpecker holes. The preference of woodpeckers for aspens has been noted by many investigators (Bent 1939, McLaren 1963, Lawrence 1966, Haapanen 1965, Kilham 1971a).

Table 16. Resistance of some Northwestern trees to fungal attack (Boyce 1961).

Very Durable	Durable	Moderately Durable	Non-Durable	Perishable
yew	western red cedar white oak	douglas fir larch ponderosa pine	hemlock spruce silver fir	alder willow

The effect of fungus on infected wood varies with the species of fungus. Fungi which cause brown rots result in wood with abnormal longitudinal swelling and shrinkage giving rise to a cubical checking pattern and considerable strength reduction of the wood. White rotted wood has normal shrinkage properties and slight strength reduction (Smith 1970). The white rots probably create more suitable excavation sites. Different species of fungi attack sapwood, heartwood, dead trees, and live trees (Boyce 1961).

Fomes ignarius, the false tinder, is a white rot of a variety of hardwoods, especially aspens; it seems to create a wood condition ideal for cavity excavating. The heartwood is softened by the decay but the sapwood remains as a tough outer shell which protects the nest cavity.

Fomes pini is another fungus which creates good excavating conditions (Steirly 1957, Ligon 1970). This species attacks almost all North American conifers while they are still living. It is particularly severe on douglas fir, larches, pines, and spruces; in many stands 50 percent or more of the trees may be infected. Swollen knots or conks often appear on the bark soon after infection occurs. The rotted wood remains fairly firm and uniform in texture (Boyce 1961).

Fomes applanatus, shelf fungus, rots heartwood; it is found mainly on standing dead trees, and creates favorable conditions for excavating. The heartwood becomes bleached and soft and spongy.

A species which creates unfavorable excavating conditions is Echinodontium tinctorium, brown stringy rot. It attacks the heartwood of hemlocks, engelmann spruce, douglas fir, and white fir. The rot creates small radial burrows and separations along the annual rings. The wood becomes very weak and fibrous. Fomes connatus which attacks hardwoods, particularly maples, also causes a stringy rot. In later stages of decay the wood may disintegrate completely leaving a hollow core.

Polyporus abietinus, purple conk, is a species which attacks dead coniferous sapwood. The wood becomes spongy or corky, honey-combed with small pockets. The hard outer shell which woodpeckers prefer is thus destroyed.

VI. IMPLICATIONS FOR TIMBER MANAGEMENT

A. Introduction

Woodpeckers throughout the world are in an increasingly vulnerable position due to man's alterations and destruction of forest systems (Tanner 1942, Campbell 1955, Vincent 1966, Thompson 1971, Short 1973). The physiognomy of the forests of the Pacific Northwest is rapidly changing due to the impacts of timber harvest and intensive timber management. Inevitably with these changes the species composition of the forest avifauna is altered. It is unlikely that any amount of wildlife management will ever be able to restore or maintain in a forest managed for timber production the avifauna supported by a natural forest. The components of forest systems are too complex and interrelated to be duplicated by even the most sophisticated management program. Even if a bird's habitat is not destroyed, alterations often reduce some necessary resource to a level at which it is impossible for the bird to maintain itself.

B. Importance of Dead and Decaying Wood

Certain gross differences between managed and natural forests are easily recognized by humans. One of the most easily recognizable differences is the disappearance of dead wood, both standing and fallen, from managed forests. It is removed in order to utilize as much space as possible to grow merchantable timber. Dead wood has variously been reported as a fire hazard, a breeding ground for forest insects and fungal infection, as interfering with broadcast burning, with aerial spraying, replanting, and timber harvest techniques (National Forest Manual 1911, Gale 1973, Gale et al. 1973). Standing dead trees are dangerous for loggers to work around (Oregon Safety Code 1969).

Under natural conditions the forest, especially a mature forest, contains many trees with soft rotten heartwood, dead-topped trees, and trees harboring bark and wood boring insects. Woodpeckers are closely associated with these components of the forest system. The basic conflict between woodpeckers and timber management is that the type of forest most woodpeckers prefer is low in economic value.

Intensive timber management in Finland significantly reduced the density of woodpeckers and other cavity nesting birds (44 to 68 percent decrease) in the forest (Haapanen 1965). The cavity nesters as a group were much more severely affected than were the open nesting birds (0 to 5 percent decrease). In both European and American forests intensive management includes removal of deciduous trees, periodic thinning, and felling of standing dead trees (Section IV. B).

Leaving some or even all dead trees standing after clear-cutting or partial cutting is a stop-gap measure not a solution. Standing dead trees are an important part of the habitat of all woodpeckers but each species also has other more specific requirements--these include fallen dead wood, sap trees, cone crops, mast crops, and occasional outbreaks of forest insects. Dead trees standing in a clearing attract a different avifauna than dead trees standing in a patch of alder or a mature douglas fir forest. Bird species are generally adapted to a certain forest structure and degree of canopy closure (MacArthur and MacArthur 1961). Flickers, bluebirds, and tree swallows might use snags in a clear cut; the starling, an extremely successful and aggressive cavity nesting species, can be expected to monopolize a large portion of the nest sites in any open area (McLaren 1963).

The question "How many snags per acre shall we leave?" has been of recent concern to resource managers. Gale (1973) found an average of 7 to 13 standing dead trees per hectare in his study areas in northern California; 20 to 70 percent of these trees were being used for nesting. Rather than being in excess, the unused trees may have been unsuitable for excavation. Standing dead trees vary in height, diameter and in species. Other more subtle characteristics of a standing dead tree may be important to woodpeckers. The species of fungus which initiates rot determines the consistancy of the heartwood of a tree. Some species of fungus create conditions which are unsuited to hole excavation (Section IV. D). The bounding flight of woodpeckers may require that the hole face a clear space and be well above obstructions (Kelleher 1963). Choosing the proper snags to leave is beyond our present knowledge of nest site requirements; the simplest solution is to leave them all and let the birds choose.

C. Forest Land Use

In recent years, commercially valuable forest lands, public as well as private have been devoted primarily to meeting the country's demand (industry's demand?) for wood fiber. The timber industry is a basic industry and as such is important in maintaining the stability of the economy in the Northwest (Wall 1972).

In the douglas fir zone, intensive timber management includes frequent thinning, mortality salvaging, and final cuts in rotations of the most economic length, about 70 to 100 years. Efforts are made to prevent the destruction of wood fiber by fire, disease, or insect attack. Potential fuel for a fire is minimized by maintaining a clean and accessible forest. Prompt harvest of infected or infested trees is practiced in order to save the wood and prevent the build up of wood destroying insects and fungi. Any misshapen or broken trees are removed at the thinnings in order to release the highly marketable trees from competition (Worthington and Staebler 1961). These practices make good sense in the light of timber management goals, but spell disaster for the woodpeckers.

In the douglas fir zone a major change in the harvesting method, which is clearcut, burn and replant, would be required to establish any policy of leaving standing dead trees after harvest. Because harvest by partial cut is extensively practiced on the east side of the Cascades, the outlook for woodpeckers there is brighter. There also, all standing dead trees are felled on clearcuts, but allowing dead trees to remain standing is compatible with the partial cut harvesting method.

D. General Recommendations

The following recommendations would create some of the conditions which favor woodpeckers; clearly they conflict with the methods now employed in managing our forests for wood fiber production. These steps may seem impractical to forest managers but in my judgement they must be taken now if cavity nesting birds are to find suitable habitats in the future.

1. Large tracts of land, 40 hectares or more, should be placed on rotations of 100, 200, 300 years or longer and allowed to develop with a minimum of human interference. Such a policy is probably the only feasible way to provide many of the forest dwelling species with suitable habitat.
2. No standing dead trees should be cut unless absolutely necessary.

3. At precommercial thins, commercial thins, and final cuts, or at partial cuts the following trees should be left:
   a) dying trees
   b) trees showing signs of heartwood rot
   c) insect infested trees
   d) trees with distorted shape or wind breakage
   e) dead-topped trees
4. Fallen dead trees and slash should be left as foraging sites.
5. After harvest, attempts should be made to duplicate the tree species composition of a stand rather than replanting it to pure douglas fir.

E. Specific Recommendations

1. Introduction

Any discussion of woodpeckers in general necessarily obscures much relevant detail. Each species has a certain optimum niche which is by definition different from the niche of every other species. However, in most cases these details are not well understood. In part, further field research can expand our knowledge. It is foolhardy not to realize that the complexity of all the interacting aspects of a species' niche is beyond present analytic methods. We may never be capable of recreating the natural environment of an organism. With these reservations the following is a discussion of some requirements of woodpecker species which conflict with timber management.

2. Three-toed Woodpeckers

Tridactylus and *arcticus* are adapted to occasional or possibly frequent superabundances of insects to which they respond both functionally and numerically (Koplin 1972). Control or elimination of insect outbreaks by timber managers may be detrimental to these species. Insect outbreaks should be interpreted in terms of the whole forest system rather than in terms of loss of wood fiber. Natural predators such as woodpeckers and parasites can prevent epidemics from reaching pan-epidemic proportions (Section IV. C). Three-toeds make heavy use of new burns because of high insect abundances (Harry Nehls, pers. comm.). Rapid clean up and replanting of burns eliminates this source of livelihood. Burned over land is a natural component of forest systems. In some cases after a fire the vegetation should be allowed to follow its natural succession.

Both species of three-toeds prefer to forage on scaly bark trees such as spruces, hemlocks, lodgepole pine, and tamarack. The abundance of these tree species is decreasing as more and more land is planted to the commercially more valuable species such as douglas fir and ponderosa pine. The subalpine segment of their habitat is relatively undisturbed because at present it is not economically feasible to harvest timber at high elevations.

3. White-headed Woodpecker

Very little is known about this species. White-headed woodpeckers forage mainly on live trees but they require standing dead trees for nesting. They prefer to nest in a tree with a diameter at the nest hole of greater than two feet and prefer to forage on the flaky, bark of mature ponderosa pine. Under present rotation lengths none of the trees in managed stands will reach the yellow "puzzle" bark stage or a diameter greater than two feet before they are cut down. Elimination of mature ponderosa pine on most of our forest lands will severely deplete populations of white-headed woodpeckers. This species should be of particular concern to resource managers in the Northwest because Oregon and Washington comprise the major portion of its distribution.

4. Downy Woodpecker

The downy woodpecker is found mainly in deciduous trees especially in riparian habitats. Alder conversion, conifer release, and other practices which eliminate deciduous trees and shrubs reduce the availability of the downy's habitat. Buffer strips along streams provide it with habitat. Pubescens is a rare species in eastern Oregon.

5. Pileated Woodpecker

Pileatus is dependent upon mature forest, a forest type which is fast disappearing and is projected by the United States Forest Service to be almost completely eliminated (U.S.D.A. 1969). It requires large nest trees, averaging 50 cm in diameter at breast height (Conner 1973) and nests at an average height of 20 meters. The nest hole is usually within the canopy (Evelyn Bull, pers. comm.). Pileateds are capable of excavating in solid wood which has undergone little or no decay (Evelyn Bull, pers. comm.).

Pileateds are sensitive to disturbance, disappearing into the forest at the approach of humans. This bird's behavior is very unpredictable. It is usually extremely shy, being found mainly in removed, inaccessible areas; however it sometimes inhabits disturbed areas close to civilization.

Pileateds forage extensively on fallen dead wood. Burning of slash, salvaging, sanitation cuts and other procedures for maintaining a clean and accessible forest reduce the amount of fallen dead wood in its habitat.

6. Sapsuckers and Hairy Woodpecker

Little is known about the williamson's sapsucker. It often occurs in old burns. Fire prevention measures and rapid replanting have reduced the availability of this habitat type.

The red-breasted sapsucker and the hairy woodpecker do not appear to have been depleted by man's activities. Both inhabit second growth, partially thinned stands, small woodlots and other altered forest types. They do however, have requirements for standing dead trees and live trees with rotted heartwood.

The red-naped sapsucker is closely associated with aspen, either in pure or mixed stands. A policy of not disturbing aspen groves and of preserving the species composition of mixed ponderosa pine and aspen stands will benefit this species.

7. Lewis Woodpecker

Logged or burned coniferous forest is an important habitat of the lewis woodpecker but it is suitable only in the brushy stage of regrowth. The brushy stage is undesirable to the timber manager and efforts are made to eliminate it. Herbicides are applied in the early stages of regeneration of a clearcut to destroy the brush and release the conifers. Burned over lands which might naturally go through a brushy seral stage are cleared and replanted as rapidly as possible to establish stands of merchantable timber.

Livestock grazing may conflict with the needs of the lewis woodpecker for a brushy understory. Heavy grazing often destroys the native understory vegetation resulting in domination by cheat grass

(Bromus tectorum) (Franklin and Dyrness 1973). Oak groves are winter habitat for lewis and should be left undisturbed.

8. Acorn Woodpecker

The acorn woodpecker's basic requirement is for mature oak groves in a moderately dry climate. Starlings commonly compete with this species (pers. obs.).

9. Common Flicker

The flicker is very compatible with civilization and has probably benefitted from man's alterations. Flickers need openness; through agriculture, timber harvest and other land clearing projects, man has increased the amount of open space in the Northwest.

F. Epilogue

The world would go on without woodpeckers, but the jeopardy of woodpeckers is only a case in point. Forest systems are extremely complex; any alteration in a component of a forest system has many repercussions. Dead wood is one such component of forest systems; eliminate it from forest systems and one repercussion is woodpeckers are eliminated. If woodpeckers are eliminated, the cavity nesting birds dependent upon them are eliminated. Many cavity nesting species are primary predators of forest insects (Beebe 1974, unpublished manuscript). If the predators of forest insects are eliminated pan-epidemics are likely to occur. The scenario could go on. Vast tracts of timber are killed by insects. Fires rage through the expanses of dry deadened timber. The forest is destroyed. All repercussions of the seeming unrelated policy of removing standing and fallen dead wood from the forest. This description is oversimplified and perhaps somewhat fanciful, but perhaps not far from the truth.

I have discussed conflicts between human activity and natural ecosystems, but in actuality we are part of natural ecosystems. We are an extremely successful species because of our ability to manipulate our environment, but caution needs to be introduced into our manipulations. Human beings should be humble in the face of nature's complexity.

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APPENDIX: SEXUAL DIMORPHISM IN WOODPECKERS

A. Introduction

All species show morphological variation; it may be continuous or polymorphic. A special case of polymorphism, sexual dimorphism, is of common occurrence in birds. The sexes may differ in gross body size as well as in proportions of body parts. Dimorphism involving the feeding apparatus has led to investigations of sexual differences in foraging behavior of woodpeckers. Although almost all structural aspects of a woodpecker's body bear some relationship to feeding (Short 1970), the bill is the morphological character most intimately involved in foraging. In birds, bill length is almost invariably more dimorphic than are other linear dimensions (Selander 1965) (Table 17). Most investigations of sexual dimorphism in woodpeckers have been concerned with bill length differences. Other characters which have been analyzed are the tongue (Selander 1965) and the tail (Short 1970). Sexual differences in foraging have been found in almost every picid species studied. Northwestern species known to exhibit sexual differences are tridactylus, albolarvatus, villosus, and pubescens. Lewis is the only northwestern species which has been studied which appears not to exhibit sexual differences in foraging.

Table 17. Percent sexual dimorphism of body length, tail length and culmen length (male-female/female). Dimensions are mean values (in mm) (Ridgeway 1914) for subspecies or race occurring in the Northwest.

	Body Length (Skins)			Tail Length			Culmen Length			Sample Size	
	Male	Female	Percent Dimorphism	Male	Female	Percent Dimorphism	Male	Female	Percent Dimorphism	Male	Female
tridactylus	202	196	0.03	74.5	73	0.03	27.1	23.9	0.13	30	33
arcticus	220	221	--	77.9	78.8	-0.01	33	30.7	0.07	39	34
albolarvatus	216	208	0.04	80.9	82.3	-0.02	28.1	25.3	0.11	14	14
villosus	224	214	0.05	78.9	78.4	0.01	32.0	28.5	0.12	37	24
pubescens	156	157.5	-0.01	60.2	60.7	-0.01	16.8	16.1	0.04	20	20
pileatus	426	407	0.05	157.2	151.7	0.04	54.4	48.7	0.12	16	8
thyroides	208	209	--	83.2	84.1	-0.02	25.6	24.2	0.06	20	17
ruber	194	195	-0.01	74.6	75.1	-0.01	24.2	23.8	0.02	10	10
nuchalis	197	195	0.01	76.5	74.4	0.03	23.3	23	0.01	20	12
lewis	252	254	-0.01	97.3	92	0.06	29.7	28.6	0.04	16	14
formicivorus	225	227	-0.01	79.5	80.7	-0.01	29.8	28.3	0.05	20	20
auratus	280	282	-0.01	112.6	109.8	0.03	37.9	36.9	0.03	45	36

B. Food Niche Partitioning

Under conditions of sympatry the niches of males and females might be partitioned in several ways: 1) different foraging techniques, 2) different prey items, 3) different foraging substrates (species of vegetation, condition of wood), 4) different positions of substrate (foraging height, stem diameter). None of these possibilities are mutually exclusive. There is very little evidence that the sexes of woodpeckers possess different foraging techniques per se (i.e., both sexes have the same repetoire of techniques) but in many cases one sex uses a method more extensively than the other. There is also no evidence of males and females foraging on the same substrate but selecting different prey. Spatial niche partitioning is the most common; the sexes exhibit different preferences for tree species or forage at different heights. The hypothesis of niche partitioning between the sexes is easier to demonstrate than it is to disprove because there is always the possibility that investigators have not categorized foraging patterns in a way that reveals foraging differences.

C. Geographical and Seasonal Variation of Sexual Differences

The degree of sexual dimorphism in woodpecker species has been found to vary geographically and seasonally. Short's studies have demonstrated a distinct seasonal variation in wing length and tail length due to wear, and bill length due to wear, differential growth or both (Short 1970). Davis (1954) found a significant seasonal variation in bill length in avian species that shift their diet seasonally. His work suggests a correlation between morphological variation and feeding behavior, probably due to wear. Thus pooling of specimens taken throughout the year may obscure morphological differences.

Geographical variation in the extent of dimorphism may be quite pronounced in species with broad distributions (Ridgeway 1914). The 18 races of villosis all show different percent bill dimorphisms. P. a. albolarvatus exhibits an 11 percent bill dimorphism while in P. a. gravirostris it is only 8 percent.

There is abundant evidence that foraging behavior described for one avian population may not hold for other populations of the species. Birds adapt their foraging patterns to local conditions. Similarly the extent of foraging differences between the sexes has been found to vary geographically. This behavioral variation may be correlated with variation in sexual dimorphism. Among the factors affecting degree of difference in foraging pattern may be prey species composition, prey abundance, intensity of competition with closely related species, and complexity of the habitat (i.e., available foraging strata). Food niche partitioning between the sexes of pubescens, villosus, and albolarvatus has been analyzed by a number of investigators. Table 18 presents their results in simplified form for sake of comparison.

Table 18. Sexual difference in foraging pattern in *P. pubescens*, *P. villosus*, and *P. albolarvatus* showing geographical variation. This chart is a simplification which obscures relevant information.

	Foraging Site	Live or Dead Wood	Foraging Height	Foraging Technique	Tree Species
Picoides pubescens					
Winter and spring in Illinois (Willson 1970)	yes	yes	yes	N. S.	yes
Year around in Kansas (Jackson 1970)	yes	yes	yes	N. S.	yes
Winter in New York (Kisiel 1972)	yes	N. S.	-	yes	yes
Winter in New Hampshire (Kilham 1970)	yes	-	yes	-	-
Late summer and winter in Colorado (Koplin 1967)	N. S.	N. S.	N. S.	N. S.	N. S.
Picoides villosus					
Winter in New York (Kisiel 1972)	yes	yes	-	N. S.	yes
Winter in New Hampshire (Kilham 1965)	-	-	-	yes	yes
Late summer and winter in Colorado (Koplin 1967)	N. S.	N. S.	N. S.	N. S.	N. S.
Picoides albolarvatus					
Spring and summer in Idaho (Ligon 1973)	-	-	N. S.	N. S.	-
Spring in California (Koch et al. 1970)	-	-	yes	yes	-

Although _villosus_ and _pubescens_ show pronounced foraging differences between the sexes in most habitats in which they have been studied Koplin (1967) found no significant differences in an engelmann spruce-subalpine fir forest. He suggested that the spruce-fir forest offers so few foraging strata for the hairy and downy woodpeckers that sexual dimorphism is of little adaptive value in reducing intersexual competition. _Villosus_ and _pubescens_ are fugitive species in subalpine forests. They are not closely adapted to foraging in this habitat so it is not surprising that niche partitioning does not occur.

The white-headed woodpecker shows distinct partitioning of its food niche in southern California (Koch et al. 1970) but Ligon (1973) found no differences between the sexes in a study conducted in Idaho. Ligon suggests that during the winter months in Idaho no partitioning could occur because only one food source, pine seeds, is available in sufficient quantities.

Although most investigations have been conducted during the winter, there is evidence that the degree of non-overlap in foraging patterns varies seasonally. Willson (1970) compared winter and spring foraging patterns of two woodpecker species and found sexual differences less pronounced in the spring. She suggested that this difference may have been due to more abundant food in the spring or that pair formation lead to greater tolerance of male and female for each other.

Koplin (1967) found that differences in foraging behavior between the sexes of the northern three-toed were least pronounced when insect prey was most abundant (late summer) and greatest when it was least abundant (winter). During the winter males spent 100 percent of their time on tree trunks; females spent 62 percent of their time on trunks, 24 percent on branches, and 14 percent on twigs. During later summer both sexes concentrated about equally on trunks.

D. Correlations of Morphology with Behavior

Although some studies have demonstrated a correlation between sexual differences in morphology and foraging behavior (Selander 1965, Koplin 1967), such is not always the case. Sexual dimorphism may exist without any evidence of niche partitioning. Albolarvatus in Idaho exhibits an 11 percent difference in bill length but at least during April through August Ligon found no foraging differences. Behavioral differences may result in intersexual niche partitioning without necessarily involving sexual dimorphism. The size differences between the sexes of pubescens are statistically insignificant (Koplin 1967) yet Kisiel (1972) found more overall differences in foraging behavior between the sexes of the downy than between the species pubescens and villosus. Thus one cannot predict foraging patterns in any given population by measuring the degree of sexual dimorphism in bill size.

E. Evolution of Sexual Dimorphism

Sexual dimorphism could have arisen through sexual selection or through ecological selection. Some combination of the two pressures is most likely, and its origin may be different in different species or even in different races. Even if sexual dimorphism were purely a product of sexual selection the mere fact of a difference in structure of the feeding apparatus would most likely lead to different optimal foraging patterns for the two sexes. That is, sexual selection would result in dimorphism which would lead to differential foraging.

Alternatively, differential foraging may have led to dimorphism. This would occur under ecological selection. A possible selective pressure is the reduction of intersex interference. Dominance by the male leading to frequent displacement of the female from preferred foraging sites might facilitate the divergence. Ligon (1968) found that the males of a number of *Dendrocopos* species utilize dominance to forage in the most productive portions of the trees with the female giving way and foraging in less desirable areas. Selander suggested that female woodpeckers of the two *Centurus* sp. he studied may have changed morphologically more than the males, indicating that the females have adjusted to the dominance of their mates. One would predict then that the females should be more specialized than the males. Willson's (1970) data indicate that male *pubescens* is slightly more specialized than the female and that the male and female red-bellied woodpeckers are approximately equal in specialization.

Ligon (1968) suggested that by the nature of woodpeckers' anatomical specialization, the trunk may be assumed to be the original foraging station. He cited data of Selander (1966), Kilham (1965), and Ligon (1968) as evidence that males forage more on trunks than do females. However there are many studies indicating that the opposite case is also common; that females forage more on trunks than do males (Koch et al. 1970, Willson, 1970, Jackson 1970, Kisiel 1972).

Inadequate food resources causing selective pressure for an expanded food niche might lead to sexual dimorphism. Bock (1970) points out that this could occur only if some amount of sexual dimorphism were already present. The selection pressures of intraspecific competition can act only to increase an already established sexual dimorphism. Otherwise, in a monomorphic population a large billed female would have the same advantage as a large billed male in exploiting food unavailable to the bulk of the population.

Evidence that ecological selection has played a part in the evolution of sexual dimorphism comes from work done by Selander (1965). He found that in Centurus striatus the horny tip of the tongue of the females is about 30 percent smaller than that of the males. The specialized tongue of woodpeckers is closely adapted to foraging methods, and it is very unlikely that sexual selection operates on this character.

The occurrence of pronounced behavioral differences in foraging patterns of males and females in the absence of significant morphological differences supports the hypothesis that there is ecological pressure for niche differentiation.

Davis (1965) noted that bill size is very often the most individually variable character within avian species. He suggested this variability may minimize intraspecific competition for food. In species that have somewhat specialized foraging niches such as woodpeckers, sexual dimorphism of bill size may supplement individual variability in lessening competition for food.

F. Effect of Dimorphism on Niche Breadth

Sexual dimorphism may lead to expansion of a species' "original" niche or to its subdivision. Subdivision will reduce intersex interference. It cannot alleviate a food shortage because any increase in the type or amount of food available to a species implies an expansion of the niche.

Niche expansion through sexual dimorphism can only occur if there is enough freedom from competition with similarly foraging species to allow wider or more thorough exploitation of the food resources. Niche expansion cannot occur if the species is contained by the presence of species with similar or overlapping niches (Selander 1965). In support of this theorizing, there is evidence that island inhabiting woodpeckers are more dimorphic than closely related continental species. Selander found that among North and Central American and West Indies species of woodpeckers the greatest dimorphism is shown by three insular forms each of which is the only resident woodpecker on its island. On the basis of morphological and behavioral studies he concluded that freedom from competition with species of similar adaptive type permitted these insular forms to achieve a wider and more thorough exploitation of available food through evolutionary divergence of the sexes in foraging behavior.

Whether sexual dimorphism results in subdivision or expansion or both there must be sufficient heterogeneity of food resources to provide subniches for the two sexes. One would predict a higher incidence of sexual dimorphism in mature systems than in successional stage because mature systems tend to be more complex and more predictable and because K-selected species tend to be specialists rather than opportunists or generalists. Lewis woodpeckers are opportunistic, concentrating on temporarily abundant food items. Field observations by Bock (1970) showed that both sexes of lewis woodpeckers respond to changes in insect populations by switching to the most abundant prey species. As Bock stated, niche differences are unlikely because selection should favor the ability of both sexes to exploit the full range of food types. However, lewis woodpeckers are distinctly dimorphic in bill and tail length (Table 17).

Willson (1970) computed an index of specialization for male and female downy and red-bellied woodpeckers (Table 19). She found that the index for a species was similar to that of either of the sexes of that species. If dimorphism were by subdivision alone one would expect that each sex would be more specialized than the species as a whole. Instead she found that one sex usually uses a given niche dimension broadly, while the other sex is specialized within the range of the first. The specialization has probably led to more thorough exploitation of food resources. Willson speculated that niche segregation of sexes is more likely to involve differences in degree of specialization to a similar range, while segregation of species may involve either differences in degree of specialization or actual subdivision of the niche dimensions.

Table 19. Indices of specialization of male and female downy woodpeckers and red-bellied woodpeckers to foraging places: $J' = H'/H'\,\max$ (Willson 1970).

		Downy		Red-bellied
		Male	Female	Woodpecker
Tree type	winter	.582	.722	.664
	spring	.515	.578	.667
Feeding site	winter	.754	.588	.751
	spring	.652	.738	.738
Feeding height	winter	.822	.782	.799
	spring	.681	.801	.805

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