FORAGING BEHAVIOR AND FUNCTIONAL MORPHOLOGY OF THE BARK-FORAGING BIRDS OF THE LOUVIERE AUDUBON PRESERVE

by

John D. Petersen

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MASTER OF ARTS

in

Biology

Dr. Robert J. Sherman, Chairman

Dr. John R. Arnold

Dr. Donald E. Isaac

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FORAGEING BEHAVIOR AND FUNCTIONAL MORPHOLOGY OF THE
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ABSTRACT

A study was conducted on five bark-foraging birds
at the Bouverie Audubon Preserve in Sonoma County,
California. This study was divided into two parts.

I. An ecological study of the foraging behavior and
   mechanics of scansorial, bark-foraging birds.

   This study consisted of field observations of
   five species: Nuttall's Woodpecker, Downy Woodpecker,
   Pileated Woodpecker, Brown Creeper, and White-breasted
   Nuthatch. Observations (totalling 127 hours) were
   conducted from February through June 1985. Observational
   data were recorded and analyzed for substrate condition
   use (live vs. Dead), substrate size utilization, foraging
   behavior, and foraging orientation.

   Each substrate and foraging category was analyzed
   as to percent utilization by each species by sex where
   detectable. These data were then tested for significant
   intersexual or interspecific differences. Significant
   differences were found between species in one or more
   resource categories. Intersexual differences were found
   for the Pileated Woodpecker only.

   Niche breadth and overlap were also quantified
   for each of the resource dimensions. Results show that
   even though these birds superficially appear to be using
   the same resources, they are actually foraging in
   significantly different ways which allow for coexistence.

II. Functional morphology and adaptations to a
    bark-foraging habit.

   This study targeted selected anatomical and
   morphological characters to determine their relationship
   to the observed behaviors in part one.

   Gravitational forces acting on a scansorial bird
   were analyzed first. Anatomical and morphological
   measurements of some characters were then compared with
   the percentage use of the foraging behaviors.

   Characters measured which appear to be correlated
   with the quantified behaviors are; 1. the length of the
   tarsometatarsus, 2. bill dimensions and morphology, 3.
   weight of the bird, and 4. length of the bird. Each of
   these variables likely works in unique combination with
   the others to effect a certain degree of ecological
separation, as expressed by their behaviors, with coexisting guild members. This results in reduced competition through resource partitioning and minimum niche overlap.

Chairperson: 

M.A. Program: Biology
Sonoma State University

Date
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PART I

AN ECOLOGICAL STUDY OF THE FORAGING BEHAVIOR AND
MECHANICS OF SCANSORIAL, DARK-FORAGING BIRDS
INTRODUCTION

Of the many daily activities of a bird, the ability to acquire food within an efficient time/energy budget is of the highest priority for survival (King 1974). Though the time spent in acquisition of food varies from species to species, the individual's vitality (and often reproductive success) is linked to this effective exploitation of a particular segment of its environment. The evolutionary track of a particular species to its current trophic niche is the result of varied and complex influences. Topics of current research in this area contain components of competitive exclusion, character displacement, competitive release, adaptive radiation, and selective predation.

In response to these pressures and opportunities functional morphological characters have been selected for, over time, which allow optimum utilization of a wide range of resources. As habitat partitioning is more efficient than food-type partitioning (Schoener 1974, Cody 1974), those characters which allow for access to unexploited habitats (micro-habitats) are likely to be highly selected for. For this reason, coexisting members may appear similar in some aspects (such as those relating to anatomical adaptations for bark scaling) while dissimilar in others (such as bill size and shape).
to allow orientation and exposure to different micro-habitats. For birds which are taxonomically closely related, or with closely related foraging behaviors, differences in morphological characters are likely to be related to differences in function. These functional differences may therefore be the basis for resource partitioning in some communities. For this reason, studies in niche segregation can benefit from an understanding of the morphological basis of observed behavior.

The focus of such a study can naturally be directed to a variety of ecologically similar species. The bark foraging birds are well suited to this type of research. Besides possessing a unique locomotion which allows for direct comparisons, they are relatively easy to observe, and their behavior is perhaps easier to quantify.

Many of the studies which have been conducted in this area are directed either to spatial and temporal distribution (e.g. Miller and Bock 1972, Williams 1975, Austin 1976, Williams and Batzli 1979, Jenkins 1979) or in anatomical surveys (Shufeldt 1900, Goode 1972). Few, such as Burt (1930) and Spring (1965) have related anatomical adaptations to behavior, but in neither case was behavior quantified.

Of the over 100 birds seen annually at the Bouverie Audubon Preserve (BAP), five species are
permanent, scansorial bark foraging residents (Appendix 1). These birds, which will be used for this study, are:

1. Nuttall's Woodpecker (*Picoides nuttallii*)
2. Downy Woodpecker (*P. pubescens*)
3. Pileated Woodpecker (*Dryocopus pileatus*)
4. Brown Creeper (*Certhia americana*)
5. White-breasted Nuthatch (*Sitta carolinensis*)

Two other woodpeckers which are permanent residents of the Preserve, but not included in this study are the Northern Flicker (*Colaptes auratus*) and the Acorn Woodpecker (*Melanerpes formicivora*). These are excluded for two reasons. The basis of this study requires that all of the study birds be closely related in substrate and resource use. The Northern Flicker and Acorn Woodpecker utilize widely different food sources than the others under investigation. For example, the Acorn Woodpecker uses acorns as its major food source, along with sap from sapsucker holes and insects obtained by flycatching (Beal 1911, Ritter 1938, MacRoberts 1970). The taking of woodboring insects and larvae by scansorial gleaning or pecking is an uncommon occurrence, particularly during the winter to spring observation period. A summer shift to a greater variety of food sources has been noted by MacRoberts (1970) and Stacey and Koenig (1984). The Northern Flicker, is a predominately ground feeding bird, using its bill to probe in the soil for insects and grubs (Bent 1939). Evolved from more arboreal ancestors (Short 1971), these
"ground woodpeckers" possess functional adaptations to a terrestrial habit. Their forays into the trees are usually for territorial or courtship displays, drumming, nesting or escape.

Secondly, from an anatomical perspective, these birds are grouped separately from the more arboreal species by having the accessory semitendonosus muscle and the lack of a folding over of the frontals along their line of contact with the premaxillae (Burt 1930). Bock and Miller (1959) further describe this group as having a perching type foot.

Two other woodpeckers not included here are the Red-breasted Sapsucker (Sphyrapicus ruber) and the Hairy Woodpecker (Picoides villosus). The sapsucker is excluded because of its winter residency and spring migration, and the Hairy because of its uncommon and sporadic occurrence at the upper BAP boundary. An interesting topic of future research may be directed to interference competition from returning sapsuckers.

This study will be divided into two parts. The first will be an ecological study of the foraging of the five species. Of particular interest are those areas related to the mechanics of feeding on the bark surface, such as the amount of pecking and scaling, and the physical orientation of the birds during foraging. Other parameters will be measured to clarify the nature and degree of niche segregation and overlap.
The second part of this study will review some of the functional adaptations that these birds possess which effect niche segregation. Where possible, relationships will be integrated into behavioral/anatomical formulas.
COEXISTENCE MECHANISMS

In a study of avian community structure within a particular habitat, those birds whose territories overlap are said to coexist with one another. The nature of coexistence over time, suggests that these species separate their critical requirements (food, nesting, etc.) to such a degree that they are not in direct competition with other species. From theories originated by Grinnell (1922), direct competition would ultimately result in the competitive advantage of one species, and the elimination of the other from their common territory.

The concept of competitive exclusion, popularly credited to Gause (1934) is difficult to prove, however, particularly within avian communities. Exceptions to the principal of competitive exclusion have been shown in Drosophila species (Ayala 1969 and 1972). Udvardy (1951) suggests that while competition for food is important in bird speciation, current population distribution is more dependent on the physical environment and individual behavior.

The nature of this paper, however, is not to decide the validity of direct competition in avian communities. Instead, this paper will investigate some
of these ecological differences and the mechanisms which result in the differential exploitation of the available resources.

Detailed research of resource partitioning is available from a variety of sources (Christiansen and Fenchel 1977, Cody 1966, Cody 1974, Hespenheide 1975, MacArthur and Levins 1967, and Schoener 1974). These discuss the varied mechanisms by which members of the same community differentially utilize available resources.

By nature of the common scansorial habit of the study birds, and their similar feeding habits, resource partitioning is likely of critical importance to coexistence. The field observational format is designed to quantify some of the resource division mechanisms to see which are most functional in resource partitioning.

One way in which ecologists try to quantify the degree of similarity in resource use, as well as the amount of specialization to a particular resource is through measurement of the niche. The concept of the niche is summed by Odum (1971) as an organisms "functional role in the environment...and its position in environmental gradients of temperature, moisture, pH, soil, and other conditions of existence."

The concept of niche, formalized by Hutchinson (1957), is considered in theory to be a multi-dimensional hypervolume (Levins 1968), the size of which is
determined by the number of environmental variables necessary for the organisms survival. This naturally can include a large number of parameters, and makes the actual delineation of the niche very difficult. In practice, variables are selected which are most critical for species survival, and which can be measured along a one-dimensional resource gradient. Definitions of niche subsets, as well as problems of application, are the source of much current research (Cody 1974, Colwell and Futuyama 1971, Hardesty 1974, MacArthur 1968, Maguire 1967, Root 1967, Roughgarden 1972, and others).

The application of the niche for this study is primarily in the use of niche overlap values between species (Horn 1966). Niche overlap is a measurement of the joint use of a resource between two species, in an identical region of niche space. Additionally, I am using a modification of Levins' (1968) formula for niche breadth, as formulated by Williams (1975). This formula is a measure of the degree of specialization to a particular resource category. These measurements can then be used to help determine which resource categories are most functional in resource partitioning.
NATURAL HISTORY

Following is a summation of the natural history of the five study birds. Information is from previous reports (cited) and from personal observations obtained during field work on the Preserve.

Nuttall's Woodpecker (*Picoides nuttallii*)

The Nuttall's Woodpecker is similar in appearance to the congeneric, eastern, Ladder-backed Woodpecker and named for the famous 19th century ornithologist Thomas Nuttall. It is easily distinguished by the transverse black and white barring on the back, black and white face, black cap, and red patch on the rear of the head in males.

The Nuttall's Woodpecker ranges "from southern Oregon through interior and coastal California to northern Baja California (Rancho Rosarito)" (Short 1982). The oak woodland is the Nuttall's primary habitat (Miller 1951), but it is also associated with "chaparral and deciduous trees bordering narrow stream beds" (Dawson 1923). Grinnell, Dixon and Linsdale (1930) reported that in addition to the Valley and Blue Oaks, the Nuttall's was found frequently in Sycamore and Cottonwood, but rarely in Digger or Yellow Pines.

Occurrence at BAP showed a primarily oak woodland
association, with territory directed along Stuart Creek.

In Miller and Bock's (1972) study of the Nuttall's Woodpecker at the Hastings Reservation, oak species were shown to be the preferential substrate, both in availability and utilization, though there was a slight seasonal shift away from oaks from July-November.

The following food items, are from Beal (1911) and based on the examination of 53 stomachs of birds. Of the total, 79% was animal matter. Coleoptera was the largest component at 29%. Hemiptera and various caterpillars comprised 15% and 14% respectively, while ants composed 8% of the diet. A variety of other insects, and spiders made up the rest of the animal food. Of the 21% vegetable matter, 8% was from fruit, while various mast, Poison Oak berries etc. comprised the remainder. This composition was found to be similar to the food of the Downy Woodpecker.

Sexual differences in foraging behavior by Nuttall's Woodpeckers have been note by Jenkins (1979). He relates the use of smaller twigs and branches by the female as the significant factor and notes a variety of foraging techniques used for the acquisition of surface and subsurface insects. Miller and Bock (1972) found difficulty in quantifying foraging behavior because of the "multiplicity of foraging methods." Jenkins (1979) quantified foraging techniques into tapping, probing and gleaning categories for both males and females. In his
study, males tapped significantly greater than females (40.2% / 29.9%), while females gleaned more than males (39.6% / 27.5%). No significant difference was found for probing. Jenkins noted however the difficulty of interpretation of sexual differences, concluding that differences in foraging technique are likely in response to differences in substrate size use.

Hutall's Woodpeckers are thought to be permanently paired, with loosely maintained pair bond through the winter (Short 1982). At BAP, they occupy the same general range throughout the year. I observed that pairs were almost always within vocal contact while foraging, often uttering a short "prrip" back and forth.

The nest is excavated in February-March (Terres 1980) with both the male and female joining in the duties. Three to five eggs are laid, largely between March 25 to June 14. The incubation time is approximately 14 days and shared by both sexes (Bent 1939). I was unable to locate the nest site at BAP. I believe that it was out of the preserve boundaries, nearer the lower section of Stuart Creek. Successful breeding was indicated by the sighting of one immature male with adults on 11 June 1985.

Territory area was estimated by Miller and Bock (1972) as about .5 miles in diameter, and roughly circular along creek drainages.
Downy Woodpecker (*Picoides pubescens*)

The Downy Woodpecker, congeneric with the above Nuttall's, is separated in the field by its white back, (shared only with the Hairy Woodpecker) white spotting on the wings, black main tail feathers with barred outer white ones, small bill, and small red occiput in the male.

The range of the Downy Woodpecker "extends across North America from southeastern Alaska, southern Mackenzie, Alberta, Saskatchewan, James Bay, and southern Quebec to Newfoundland; thence south in woodlands, cultivated areas, and forests to southern California, central Arizona, northern New Mexico, Oklahoma, south-central Texas, the Gulf Coast, and Florida" (Short 1982). Its habitat preferences are very diverse; from open woodland to riparian, small woodlots, orchards, and city parks (Terres 1980).

At BAP, the pair of resident Downys show a preference for the Riparian Woodland and adjacent Mixed Evergreen Forest. Some forays were made into the Oak Woodland community. Nesting location was approximately 50m from Stuart Creek in a dead branch of Bay Laurel.

Beal, (1911) in his examination of 723 stomachs from birds in the eastern U.S., found the Downy's diet to consist of 76% animal matter and 24% vegetable matter.
Of the insects taken, 22% were beetles, of which 14% were woodboring larvae.

Much of the current ecological research on Downy Woodpeckers addresses differences in male/female behaviors (Grubb 1975, Jackson 1969, Kilham 1970, Kisiel 1972, Williams 1975, Wilson 1970). In each of these investigations, sexual differences in foraging behavior have been found in at least one of the following areas: 1. plant species used, and/or live vs. dead substrate; 2. method of foraging; and 3. feeding sites (vertical or limb size distribution).

Generally speaking, the Downy forages in a similar manner to the Nuttall's, scaling the bark surface, stopping to probe in a crevice, or digging out an insect or grub. Words such as diligence, industrious and perseverance have been often used to describe the character of this bird.

Drumming usually commences in the early spring, which serves to announce territoriality, renew pair bond, or attract unmated birds (Kilham 1962). At BAP, drumming by Downy Woodpeckers was first noted in mid-March, with both sexes drumming, sometimes together on the same tree. Typical behavior was a fast roll of about one second, followed by a 5-10 second interval of waiting and looking around. Drumming was exclusively on dead substrate.

Tapping, as differentiated from drumming by longer, slower duration is related to the actual nest
The nest is excavated by both sexes, with the nest site ranging from 8 to 50 feet above the ground, often in a dead or dying branch or stub. (Bent 1939) As mentioned above, this corresponds well with the Downy pair at UAP, which built their nest in the top of a dead branch about 30 feet above the ground. Four or five eggs are average, incubation is 12 days, and the young are fledged 21-24 days after hatching. My observations show that both sexes feed the young, with a parent carrying food to the nest hole every 1-3 minutes during the height of feeding.

Pileated Woodpecker (Dryocopus pileatus)

The Pileated Woodpecker, one of the largest North American woodpeckers, is a spectacular bird of the forests. Though closely resembling the nearly extinct Ivory-billed Woodpecker (Campephilus principalis), of which a few individuals are believed to exist in Cuba, these two species are derived from different ancestral groups (Goodge 1972). Field identification is derived from the large size, (40 to 50 mm long) solid black back, prominent red crest in both sexes (the back half only in the female), and a prominent mustache; red in the male, black in the female. The large, white front half of the wing is diagnostic in flight.
The Pileated Woodpecker is resident in the "forests of North America from northern British Columbia and southern Mackenzie across southern Canada to central Quebec and Nova Scotia, ranging south to northern California, Oregon, Idaho, Montana (rarely a vagrant to Arizona, New Mexico, Utah), southern Manitoba, and southward east of the Great Plains to eastern North Dakota, eastern Kansas, eastern Oklahoma, and eastern Texas, thence eastward to the Atlantic Coast and south to the Gulf Coast and Florida" (Short 1982).

In all accounts they prefer extensive stands of forest, both coniferous and broadleaf, (Bock and Lepthien 1975) but are reportedly adapting to less "primeval" conditions and to second growth forest (Bent 1939). They are often found in areas of dead or decaying trees, presumably because of the abundant food supply in the decaying wood.

At BAP, they are primarily associated with the Mixed Evergreen Forest plant community. My observations show that dead substrate is used almost exclusively, whether it be a dead tree or the dead branch of a live tree. Douglas Firs appear to be a favorite. Also, dead portions of Madrone and Quercus species have been utilized. Main activity appears to be directed around the 2km. length of Stuart Creek canyon.

In an examination of 80 stomachs, Beal (1911) found that 73% was animal matter and 27% wild fruit,
seeds etc. Of the animal matter, ants comprised some 40% of the total, with beetles and wood-boring larvae adding 22%. Miscellaneous surface animal food accounted for only 11%. Bryant (1916) noted the large number of carpenter ants in birds taken in Lake County and near Yosemite Park. A.L. Nelson's 1887 biological survey in northern Canada, as reported in Beal (1939), showed 60% large black ants as the average in the 23 stomachs tested. As illustrated, sub-surface food items, particularly carpenter ants, contribute a major portion of the Pileated's diet. It is understandable then, why a large foraging range with sufficient dead wood is required for survival of this species.

Foraging behavior is largely a reflection of the sub-surface feeding pattern. Few foraging studies have been done on this species, undoubtedly because of its uncommon occurrence, large foraging range, and shy demeanor. The pair at BAP are no exception, but I have been fortunate to view them for extended periods and have made the following observations: much time is spent in pecking and excavation of trunks and branches; large holes in some of the dead trees are evidence of their perserverance; and percussion is loud, and not as rapid as in the Nuttall's or Downy Woodpeckers. The Pileated Woodpecker will often strike the substrate at an oblique angle, widening a crevice or peeling off bark to expose inner food items. I have observed a male stripping over
1.5 meters of bark off a dead Douglas Fir branch. It then pounded a few times on the exposed surface and laid its bill sideways to the surface, presumably to use its tongue to retrieve food from within the cavity. It would then repeat this pecking and feeding process along the branch and at different angles. As confirmed by others (various reports in Bent) this bird will forage to ground level, and has been observed at BAP at the base of various dead Madrones.

The nest hole is usually located in a dead tree, or the dead portion of a live tree (Bent 1939, Bull and Meslow 1977). Many tree species may be used, but they may prefer those close to water (Hoyt 1957, Conner et al. 1974). Both sexes contribute to nest building. Three to four eggs are usually laid, with an incubation period of 18 days (Hoyt 1957). Both sexes feed the young, and have been variously described as "doting parents".

I was not able to locate the nest hole at BAP, which is not surprising considering the probable territory size. Neither has successful breeding been confirmed, as no young have been seen, nor have observations indicated that the adults have been in a nestling-feeding cycle.
White-breasted Nuthatch (*Sitta carolinensis*)

The White-breasted Nuthatch is resident "from southern British Columbia, southeastern Alberta, northwestern and central Montana, southern Manitoba, southern Ontario, southern Quebec, northern Mackenzie, northern and central New Brunswick, Prince Edward Island, Cape Breton Island, and central Nova Scotia, south to southern Baja California, southern Mexico; absent from most of the Great Plains of the U.S." (Terres 1980).

A small bird, 13 - 15 mm long, it is distinguished by its black cap and nape, blue-gray unstreaked back, white face and underside, black and white tail, and long straight bill. It is the largest North American nuthatch, and easily told from other birds by its habit of walking downward along tree trunks and branches. Its familiar "yank yank" call is a common sound in most woodlands.

Perhaps the most unique feature of this bird is its ability to move head first, downward on the bark surface. This orientation to the substrate is believed to expose prey items different from those encountered in the head-up movement (Allen 1912). The ability to move in this direction is a result of special morphological adaptations. Specifically, the increase in the relative length of the tibiotarsus (20% in *Sitta europaea*; Norberg 1981) coupled with the long curved claws, allows the bird to transverse the substrate with a walking movement,
rather than by hopping as in the woodpeckers. Forbush (1929) describes the three fore-claws of the upper foot being turned backwards during downward movement. Some photographs confirm this position, though I am not aware of the extent of its use.

Feeding habits are seasonal, with insects comprising the majority of the spring and summer diet, and vegetable matter dominating in the fall and winter (Terres 1980). Williams and Batzli (1979) in their study of the winter diet in central Illinois, found 20.2% animal matter, almost entirely insects. Hymenoptera adults comprised the largest percentage (7.2%) and Coleoptera adults second (6.5%). Vegetable matter totaled 71.8%, with the largest portion being Zea mays (49.7%). No mention was made in this study as to the relationship of this data to the total annual food percentages.

Personal observations at BAP from February through June show these birds to be feeding primarily on bark dwelling insects and their larvae. A few times they have been observed feeding on nuts of an unknown variety, but have not been seen taking other vegetable matter.

Nests are usually located in tree cavities, whether natural, excavated or abandoned by a woodpecker (Brewster 1906; Terres 1930). At the Bouverie Preserve, a pair built their nest in the rotted trunk of a Blue Oak, approximately 1.5 meters off the ground.
Between five to ten eggs are laid, and hatch after 12 days of incubation, which is shared by both sexes (Bent, 1939). The young, which closely resemble the parents, are able to fly approximately 14 days after hatching (Terres 1980).

Brown Creeper (Certhia americana)

The Brown Creeper is resident from "south-central and southeast Alaska across southern Canada to Newfoundland southern Alaska, across southern Canada to Newfoundland; in West, south to southern California, through Mexico to Nicaragua; in East, south in Appalachians to eastern Tennessee and west North Carolina" (Terres 1980). Their habitat preference is for stands of mature hardwoods or conifers.

The appearance of the Brown Creeper closely resembles the bark surface on which it feeds. It is 13-15 mm long, with mottled brown upperparts, white below, a slender downcurved bill, and a long, stiff tail. Its call consists of a thin, high-pitched "tss" which it makes regularly while foraging, and which apparently also acts as a location call to its mate. This bird would be much more difficult to find in the field were it not for this distinctive call.
One distinctive behavioral feature of the Brown Creeper which is described in the literature is its habit of flying to the base of a tree and spiraling up towards the top, then flying to the base of a nearby tree and repeating this movement. My observations show a great variation from this classic description. Though this movement is relatively common, these birds will often move straight up one side of a tree without exploring the other side. A few times they were observed in the early morning foraging among Douglas Firs, and climbing only on the shaded side of the tree. Often on some of the larger oaks they would forage from a main junction on the tree to the outer limbs, then return to the same junction and leave on a different route. This could continue on the same tree for well over 15 minutes. Foraging on the undersides of limbs was also a common occurrence. Flycatching was observed infrequently.

During foraging, these birds were observed to be in an almost constant state of movement, both with their bodies and with their heads; moving back and forth, scrutinizing each hole and crevice. While resting, they prop themselves motionless on a trunk and seemingly blend into the wood surface. Roosting is done in a similar manner.

Food items were analyzed for the winter diet in a central Illinois woodland (Williams and Batzli 1979). Their study found 92.0% of the food in the five examined
stomachs to be animal matter. Hemiptera was 22.8% of the total, 34.4% was Homoptera, 12.4% was Coleoptera, and 11.6% was Araneida. McAtee (1926) and Stoner (1932) both note the value of this bird in feeding on insects which are destructive to trees.

The Brown Creeper usually builds its nest in either a rotted cavity in a tree, an abandoned woodpecker hole, or more often behind a loose strip of bark on a live or dead tree. The nest is lined with feathers, grasses, lichens, mosses and shreds of bark (Terres 1980).

Two nests were observed on the Bouverie Preserve, each within 100 meters of the other. One was approximately eight meters up, behind a bark shelf in a live Redwood. The second nest was 15 meters off the ground, behind a section of loose bark in a dead Douglas Fir. In neither case was nesting material observable.

Clutch size ranges from four to eight eggs, with five to six being most frequent. The eggs are incubated 14-15 days (Terres 1980). The young leave the nest after 13-14 days (Bent 1939).
DESCRIPTION OF STUDY AREA

The study area is located on the property of the Bouverie Audubon Preserve (BAP). This preserve is in the southeast corner of Sonoma County, California; near the town of Glen Ellen, approximately 20 kilometers from Santa Rosa and 10 kilometers from Sonoma, east of Highway 12 (Map 1). The preserve itself consists of about 160 hectares of land representing 5 major plant communities; Valley Grassland, Northern Oak Woodland, Mixed Evergreen Forest, Chaparral (Munz and Keck 1968), and riparian woodland (Ornduff 1974). Topography ranges from the level grassland to steep canyon walls (Map 2). Geology of the preserve shows a volcanic origin of the underlying rock; rhyolite and fractured basalt (Frazier and Frazier 1978). Four major soil types are represented; Red Hill clay loam, Goulding cobbly clay loam, Goulding-Toomes complex, and Forward gravelly loam (Frazier and Frazier 1978).

The study area includes approximately 50 hectares of varied terrain (Map 3). Three plant communities are represented. Ornduff (1974) defines a plant community as "a regional assemblage of interacting plant species characterized by the presence of one or more dominant species". Map 4 shows the distribution of these communities. The largest plant community in the study
MAP 1. Location of the Bouverie Audubon Preserve.
MAP 2. Map of the Louverie Audubon Preserve and adjacent area. The preserve lies in portions of sections 11, 14, and 15 of township 6 N, range 6 W, Mt. Diablo base and meridian. Preserve boundary is outlined in blue, study area in green.
MAP 3. Map of the study area. The boundary of the study area is in green.
MAP 4. Map of the plant communities of the study area.
Plant community descriptions are in the text.
area is the Northern Oak Woodland. Plant species were identified using Munz and Keck (1968). Oak species include Blue Oak (*Quercus douglasii*), Black Oak (*Q. kelloggii*), Coast Live Oak (*Q. agrifolia*), Interior Live Oak (*Q. wislizenii*), Valley Oak (*Q. lobata*), and Oregon Oak (*Q. garryana*). Densities range from primarily open woodland to areas of denser, thick stands. Little or no understory vegetation is present, except for some Poison Oak (*Rhus diversiloba*) on rocky outcrops. Scattered within this community in suitable areas are also California Bay (*Umbellularia californica*), California Buckeye (*Aesculus californica*), and Madrone (*Arbutus menziesii*). This community is the site of many spring wildflowers.

A Mixed Evergreen Forest community is present on the north-facing slope of the Stuart Creek canyon, as well as covering one large hill adjacent to the canyon. Species composition includes dense stands of Madrone, California Bay, Interior Live Oak, Coast Live Oak, Douglas Fir (*Pseudostuga menziesii*), and two small groves of Redwood (*Sequoia sempervirens*). A dense to partially open understory is composed of Poison Oak (*Rhus diversiloba*), Toyon (*Heteromeles arbutifolia*), Manzanita (*Arctostaphylos manzanita*), Wood Rose (*Rosa gymnocarpa*) and several fern species.

The third plant community is the Riparian Woodland. This vegetation, associated with Stuart Creek,
is a narrow corridor of White Alder (*Alnus rhombifolia*), Bigleaf Maple (*Acer macrophyllum*), California Bay, and some Oregon Ash (*Fraxinus latifolia*). The streambed contains three sedge varieties (*Carex* spp.), and Scouring Rush (*Equisetum telmateia*). Understory vegetation includes Blackberry (*Rubus* spp.), Poison Oak (*Rhus diversaloba*), Snowberry (*Symphoricarpos rivularis*), and Hazel nut (*Corylus cornuta* var. *californica*). Stuart Creek, which enters Sonoma Creek near Glen Ellen, is spring-fed, with a year round flow (marginal in late summer).

Included on the western edge of the study area are the houses of the Bouverie Ranch. Vegetation is very similar to the Northern Oak Woodland, as the structures were built with minimum habitat impact. This area is frequently used by some of the study birds as a part of their normal range.

Plant communities adjacent to the study areas are the Valley Grassland, and Chaparral (Munz and Keck, 1968). To my knowledge, these areas were not used by the study birds.

Climate of the preserve is typical Mediterranean, with mild wet winters, averaging 102 mm of rain per year, and hot dry summers. Fog is common in the summer mornings. Varied micro-climates occur depending on slope orientation, contour, proximity to water, and overstory vegetation.
ME'I'UA~

From late February to late June, 1965 a total of 127 hours of field observations were conducted within the study area. The purpose of these observations was to quantify the foraging behavior of the birds under investigation. Of particular interest were the foraging mechanics, movements and substrate orientation. To this end two observation forms were eventually used; the first (Appendix 2) being replaced after one month with a second more efficient format (Appendix 3). Both forms included such standard information as date, time at beginning and end of observational period, weather, and sex of bird if discernable. Each also included the tree species, and its condition; alive or dead. The primary difference between the two formats is in the method of quantification of the foraging behavior. Format 1 listed the total number of seconds within each limb diameter class, and a generalized foraging behavior for each "bout" (defined as a continuous foraging sequence, beginning upon landing on a substrate and ending upon flying or hopping to another; even if within the same tree). This method, however, proved inadequate for quantifying the relative amounts of time spent in each foraging behavior and the bird's orientation with respect to the bark surface. For this reason a different format was adopted.
which was a variation of the method of metronome timing in behavioral studies (Wiens et al. 1969). This method was more practical and manageable than continuous timing, and resulted in an organized format which is easily used to determine relative frequencies of observational data. This form recorded foraging behavior at 10 second intervals, as measured with a stopwatch. Observational categories were determined from a review of the literature, and judgement of those resource variables most important in partitioning for the species under investigation.

At each observational "point", information was recorded as to: 1. limb diameter in inches; 2. foraging behavior; and 3. foraging orientation.

Limb diameter for this study was not subdivided into trunk vs. branch vs. twig etc. "Limb" refers solely to the physical bark substrate. Limb diameter was estimated using the size of the bird (from field guide estimates given in inches) as a reference. For this reason all estimations are in inches.

Foraging behavior is defined as follows:
S = Scaling; movement (up, down or lateral) on the bark surface.
PR = Probing; a non-percussion exploration of the bark surface or sub-surface cracks, crevices etc., conducted while stationary on the substrate.
PK = Pecking; a percussionary movement of the bill
associated with subsurface feeding. This movement may be used to widen existing crevices, or to expose sub-cambial food items. Pecking intensity varied between species and occasion, but was not quantified.

Foraging orientation (Figure 1) is defined as follows:

\( V = \) Vertical; a range of angles from a head-up position perpendicular to level ground, to a back-up position parallel to level ground. This range accommodates the wide gradation of angles present in a natural branching system. This category does not include any orientation of the bird with its back or head pointing to the ground surface.

\( HD = \) Head-down; an orientation in which the body is at a greater than 45 degree angle relative to level ground, with the head directed downward.

\( BD = \) Back-down; an orientation in which the body is at an angle less than or equal to 45 degrees, relative to level ground, with the back facing to the ground surface.

Timing of birds for recording purposes was started three seconds after their landing on a substrate to allow for initiation of foraging behavior. This same interval was used for birds that were discovered in the process of foraging.

This format allows for quantification of relative times spent in each foraging activity, as well as the
FIGURE 1. Model of foraging orientation. This model was used in observational form 2. Axes represent substrate angles, and dotted lines indicate range of angles applicable to each orientation. Arrows show the relative orientation of the bird's head and body on the substrate applicable in each category. For further explanation, see text.
physical orientation.

Integration of the two observational formats is used only when the methods are identical. Because of applicability and sample size, format 2 is of greater importance to the results of this study.

Field observations were collected at all times of the day, but were more frequent in the early morning and late afternoon, as these are the times of greatest activity of diurnal birds (Lack 1954). Variations in cloud cover and wind conditions were experienced, but no observations were taken in the rain.

Observational forays were always initiated from Emily's cottage (MAP 2). Because this study is primarily concerned with foraging mechanics rather than distribution or abundance, no set transects or other designed procedures were established for sampling. Additionally, because of the limited number of study birds in residence, (1-2 pairs per species) and since most birds showed a preference for territories nearer Stuart Creek, a greater proportion of observational time was necessarily weighted in this area.
RESULTS

1. Statistical Methods

Data were recorded as described in the Methods section of the text. Sample size varied with species and sex, and is listed in the appropriate Tables.

Behavioral data were analyzed primarily as percentages of the observed behaviors. Orientation, limb diameter use and substrate condition were all analyzed in this manner.

The Chi-square test of association was performed on the data of foraging behavior, foraging orientation, limb diameter preference, using the Sonoma State University Cyber 170 computer and the Minitab statistical computing system. These tests were performed between males and females of the same species, and between each of the individual species. In these situations the null hypothesis is that there is no relationship between the sexes (species) in the observed resource category. The alternative hypothesis is that there is a relationship. (Levels of significance are given in Table 1). The null hypothesis was rejected at the .05 level of significance.
Specialization within each resource category was computed using Williams (1975) formula:

\[ B_i = \frac{1}{P_i \cdot (n)} \]

where \( P \) is the proportion of time spent in the \( i \)th category, and \( n \) equals the total number of categories in the set. \( B_{\text{max}} (=1) \) occurs when an individual uses all resource categories equally. \( B_{\text{min}} (=0) \) occurs when an individual specializes use to one resource category.

As mentioned earlier, the measurement of resource specialization (or generalization) gives a numerical representation of the range of use of the resource variables. In this study, it indicates the variety and differential use of some important resource categories functional in successful coexistence. Of the numerous resource categories, those chosen for this study are: 1. the condition of the foraging substrate, 2. foraging behavior, 3. foraging orientation, and 4. foraging on differing limb sizes.

Niche overlap is calculated using Horn's (1966) formula:

\[ R_o = \frac{\sum (x_i + y_i) \log (x_i + y_i) - \sum x_i \log x_i - y_i \log y_i}{(X \cdot Y) \log (X \cdot Y) - X \log X - Y \log Y} \]
where \( x \) and \( y \) are the proportions of time spent in the \( i \)th category of the respective samples. \( X \) and \( Y \), the total observed time for each species can then be set at \( X = Y = 1 \) when the data is in the form of frequencies. \( R \) is maximized (=1) when the two species show the same proportion of use among compared resource category. A minimum \( R \) value (=0) occurs when there is no common use of any resource category.

This measurement of niche overlap serves to quantify the joint use of the observed resource variables. Birds with large overlaps of identical resource categories are likely to be in competition for limiting resources.

2. Statistical Analysis

A variety of significant differences were found in foraging, spatial distribution and behavior for the five species under investigation. For simplification, each factor will be addressed separately, with a discussion following.

LIVE VS. DEAD SUBSTRATE USE

Substrate use was quantified on observation forms 1 and 2 for each species, and different sexes where detectable. As indicated in Figure 2, all species except
TABLE 1. Chi-square values computed from Cyber 170 computer program; Minitab "test of association". A single asterisk (*) denotes a significant difference (P<0.05) in the indicated resource state. A double asterisk (**) denotes a significant difference (P<0.01). Degrees of freedom are two for foraging behavior and foraging orientation; and five for limb diameter.

<table>
<thead>
<tr>
<th>Species/sex</th>
<th>Foraging behavior</th>
<th>Foraging orientation</th>
<th>Limb dia.</th>
</tr>
</thead>
<tbody>
<tr>
<td>NW male</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NW female</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>DW male</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>DW female</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PW male</td>
<td></td>
<td></td>
<td>**</td>
</tr>
<tr>
<td>PW female</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WBN/BC</td>
<td></td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>BC/NW</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>BC/DW</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>BC/PW</td>
<td>**</td>
<td>**</td>
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<tr>
<td>WBN/NW</td>
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<td>**</td>
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<tr>
<td>WBN/DW</td>
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<tr>
<td>WBN/PW</td>
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<tr>
<td>DW/NW</td>
<td></td>
<td>*</td>
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<tr>
<td>PW/NW</td>
<td>**</td>
<td>*</td>
<td>**</td>
</tr>
<tr>
<td>PW/DW</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
</tbody>
</table>
FIGURE 2. Histograms of condition. This graphs the condition (live vs. dead), of substrate used by the study birds. Use is listed as a percentage of the total. Sexes are represented separately for the woodpeckers. Sample size, "n", is listed for each species.
SUBSTATE CONDITION

- Nuttall's
  - Male: n = 470
  - Female: n = 538

- Downy
  - Male: n = 373
  - Female: n = 213

- Pleated
  - Male: n = 321
  - Female: n = 213

- Brown Creeper
  - n = 738

- White-breasted Nuthatch
  - n = 771
the Pileated Woodpecker used live wood more than 88\% of the time. The Pileated showed the greatest use of dead substrate, with a combined average of 65\% for both sexes. This preferential use of dead wood is likely a reason for its relatively large territory size. As dead trees comprise a small percentage of most forests, a much larger area is required than for a similar number of live trees.

It is possible that the Nuttall's and Downy Woodpeckers, and the Brown Creeper and White-breasted Nuthatch use dead substrate in approximate proportion to its occurrence in the forest. This would suggest a random selectivity of trees by these birds. An alternative possibility is that they prefer live trees either because of the prey items encountered there, or the predator protection provided by the leaves. Further study is required for this question, including the density of live and dead trees in the study area.

SUBSTRATE SIZE UTILIZATION

Table 2 lists the percentages of substrate use for each of the five species. Figure 3 shows substrate use as a function of limb diameter. Males and females were graphed separately for the woodpeckers.

Comparison of these graphs shows the Brown
| Limb dia. (inches) | >1 | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | >24 | n  |
|-------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| Nuttall's♂        | -  | 11 | 8  | 15 | 19 | 14 | 9  | 3  | 7  | 2  | 5  | 1  | 2  | -  | 2  | 1  | -  | -  | -  | -  | -  | -  | -  | -  | -  | 1  | -  | 165 |
| Nuttall's♀        | 1  | 2  | 11 | 20 | 30 | 11 | 17 | 4  | 3  | 1  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | 205 |
| Combined          | .5 | 6  | 10 | 18 | 25 | 12 | 14 | 4  | 5  | 1  | 2  | 1  | 1  | -  | 1  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | 370 |
| Downy♂           | 2  | 1  | 11 | 12 | 6  | 4  | 1  | 3  | 2  | 7  | 3  | 5  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | 154 |
| Downy♀           | -  | 6  | 34 | 32 | 10 | 4  | 4  | 4  | 4  | -  | 2  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | 45  |
| Combined          | 1  | 10 | 25 | 22 | 12 | 5  | 4  | 2  | 3  | 2  | 6  | 2  | 3  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | -  | 45  |
| Pileated♂        | -  | -  | -  | 3  | 4  | 1  | 13 | 4  | -  | 7  | 4  | 13 | -  | 6  | 30 | 4  | -  | 7  | -  | 3  | -  | -  | -  | -  | 1  | 73  |
| Pileated♀        | -  | -  | 2  | -  | 15 | 10 | 7  | 7  | 3  | 10 | 3  | 14 | 1  | 12 | 2  | 1  | 1  | -  | -  | 1  | 1  | 1  | -  | -  | -  | -  | 203 |
| Combined          | -  | 1  | -  | 12 | 14 | 6  | 9  | 4  | -  | 9  | 4  | 14 | -  | 11 | 9  | 2  | 1  | 2  | -  | -  | 1  | .4 | .4  | -  | -  | 276 |
| Brown Creeper♂   | 3  | 4  | 7  | 6  | 4  | 5  | 2  | 6  | -  | 6  | 2  | 11 | 1  | 7  | 1  | 4  | 1  | 7  | -  | 10 | 1  | 4  | -  | -  | 3  | 5  | 420 |
| White-breasted♂  | 1  | 7  | 12 | 17 | 17 | 7  | 10 | 3  | 6  | -  | 3  | 1  | 7  | 1  | 2  | 2  | 1  | -  | -  | -  | -  | 1  | -  | -  | -  | 412 |
| Nuthatch         |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    | 48  |
FIGURE 3. Substrate size utilization. This is graphed as percent use by each of the study birds. Males and females are listed separately for the woodpeckers.
Creeper to be a far greater generalist than any of the other birds in limb size use. Only the Nuttall's and male Pileated showed a greater than 50% utilization in any one diameter class. This was in the 3-5" class for the Nuttall's, and the 11-15" class for the male Pileated. In addition, both the male and female Pileated showed a general preference towards the relatively larger limb diameters, with a combined foraging average of 73% on limbs larger than 5". The Downy showed the greatest preference for smaller limbs, with an average 36% of foraging done on limbs <3" in diameter. The White-breasted Nuthatch expressed limb size utilization similar to the Nuttall's.

Sexual differences were not significant for either the Nuttall's or Downy, but were significant for the male and female Pileated Woodpecker (Table 1). The female was found to use a greater percent of smaller (3-5") limbs than the male. Significant differences were found between all species except between the Nuttall's Woodpecker and the White-breasted Nuthatch, and between the Downy Woodpecker and the White-breasted Nuthatch (Table 1).

FORAGING BEHAVIOR

Quantification of foraging behavior was very helpful in understanding the dynamics of coexistence
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<th>Head down</th>
<th>Back down</th>
<th>Total scaling</th>
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<tbody>
<tr>
<td><strong>Nuttall's male</strong></td>
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<td>0.6</td>
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<td>46.0</td>
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<tr>
<td>female</td>
<td>30.2</td>
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<td>combined</td>
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<td>1.4</td>
<td>3.0</td>
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<tr>
<td><strong>Downy</strong></td>
<td>37.7</td>
<td>0.6</td>
<td>13.6</td>
<td>51.9</td>
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<tr>
<td>female</td>
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<tr>
<td><strong>White-breasted Nuthatch</strong></td>
<td>37.4</td>
<td>21.1</td>
<td>9.5</td>
<td>68.0</td>
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Table 3b: PROBING

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<th>Vertical</th>
<th>Head down</th>
<th>Back down</th>
<th>Total probing</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Nuttall's</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>29.7</td>
<td>1.8</td>
<td>6.1</td>
<td>37.6</td>
</tr>
<tr>
<td>Female</td>
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<td>Back down</td>
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<td><strong>Nuthatch</strong></td>
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FIGURE 4. Histogram of foraging behavior. Sexes are graphed separately for the woodpeckers. Each graph shows scaling, probing, and pecking as a percentage of the combined behaviors. "n" is the sample size for each species.
FORAGING BEHAVIOR

Nuttall's

- male, n = 185
- female, n = 205

Downy

- male, n = 154
- female, n = 45

Pileated

- male, n = 73
- female, n = 203

Brown Creeper

- n = 420

White-breasted Nuthatch

- n = 412
mechanisms and niche segregation. Tables 3a, 3b, and 3c list the percent use of the foraging behaviors and orientation for each of the study birds. Male and females are listed separately for the woodpeckers, with a following row for combined use.

Figure 4 illustrates the percent use of the three foraging behaviors: scale, probe and peck for each of the five species. Chi-square values are listed in Table 1.

Of the three woodpecker species, no significant intersexual differences in foraging behavior were found. The lack of significant differences in foraging behavior for the sexually dimorphic Woodpeckers, as reported in other studies, may be a function of the season. Sexual dimorphism is generally a mechanism to reduce intersexual competition for food (Selander 1966). During times of plentiful food supply, as during the spring sampling, such competition may be lessened. Also, similar foraging behavior may still result in different food items being utilized.

In any case, my findings of behavioral use for the Downy were very similar to Jackson's (1970) results at the University of Kansas Natural History Reservation. Specifically, comparisons of the two findings for BAP/UK are: 1.) scaling, male- 51.9/51.3; female- 46.8/41.7. 2.) probing, male- 32.4/34.8; female- 35.6/43.3. 3.) Pecking, male-15.5/14.0; female- 15.6/15.0. As vegetation species composition is very different between the two areas,
similarities likely reflect efficient foraging mechanics.

The Pileated Woodpecker pecked considerably more than any other species, totaling 45% of the foraging time. Conversely, the Pileated utilized scaling less than any others. The Brown Creeper scaled the most often of all, while pecking the least. Significant interspecific differences in foraging behavior were found between all species, except between the Brown Creeper and White-breasted Nuthatch, and between the Nuttall's and Downy Woodpeckers.

FORAGING ORIENTATION

Figure 5 shows the percent use of the different foraging orientations: vertical, head-down and back-down separately for each species. Chi-square values are shown in Table 1. The White-breasted Nuthatch showed a much greater use of the head-down and back-down positions (46% combined) than any other. The Brown Creeper and Downy Woodpecker showed a very similar foraging orientation, with both using the back-down position greater than any other species.

There was no significant difference in foraging orientation between the woodpecker sexes. However, significant differences were found in foraging orientation between all species except between the Downy
FIGURE 5. Histogram of foraging orientation. Males and females are graphed separately for the woodpeckers. Each orientation is shown as a percentage of the total.
Nuttall's
- male
- female

Downy
- male
- female

Pileated
- male
- female

Brown Creeper

White-breasted Nuthatch

ORIENTATION
Woodpecker and the Brown Creeper, and between the Nuttall's Woodpecker and the Brown Creeper.

RESOURCE SPECIALIZATION

Resource specialization was computed using Williams (1975) formula. This formula is given and discussed earlier in this section. It is used here as a measurement of the usage range of a resource variable (Table 4).

Mean values are similar for all species, though there are differences within each resource category. Ranking of these species from most to least specialized is as follows: Nuttall's Woodpecker, White-breasted Nuthatch, Brown Creeper, Downy Woodpecker, Pileated Woodpecker. Such a ranking may be misleading, however, as the mean numbers are very close and don't necessarily reflect the great degree of specialization within certain categories.

Limb diameter preference showed the greatest amount of specialization, while foraging behavior showed the least. The Nuttall's showed greatest specialization in limb diameter, with foraging orientation second. Foraging behavior was the least specialized for the Nuttall's. The Downy showed ranked categories identical to the Nuttall's, though it tended to be slightly more of a generalist. The Pileated was most specialized in
foraging orientation, (using the vertical position).
Substrate condition (live vs. dead) was the least
specialized category. The Brown Creeper showed the least
category deviation from its mean. It was least
specialized in limb diameter use, perhaps reflecting its
greater scaling mode. In contrast, the White-breasted
Nuthatch specialized greatest in limb diameter, with
substrate condition second. Least specialized for the
nuthatch was foraging orientation, which reflects the
often used head-down position.

NICHE OVERLAP

Niche overlap is calculated using Horn's (1966)
formula as indicated earlier. Niche overlap is maximized
when \( R = 1 \) and minimized when \( R = 0 \).

Table 5 lists the niche overlap for the study
species. As expected, comparisons show a high degree of
overlap between the males and females of the woodpeckers.
Similar overlap would be likely for the nuthatch and
creeper, could sexes have been determined. The greatest
overlap was found between the congeneric Downy and
Nuttall's woodpeckers. The least amount of overlap was
found between the Pileated Woodpecker and the
White-breasted Nuthatch.

By category, foraging orientation showed the
greatest degree of overlap, followed by foraging
behavior, substrate condition, and limb diameter.
### TABLE 4. Resource specialization. Computed using Williams' (1975) formula, where B max=1, and B min=0.

<table>
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<tr>
<th>Species/sex</th>
<th>Live vs. dead</th>
<th>Limb dia.</th>
<th>Foraging behavior</th>
<th>Foraging orientation</th>
<th>Mean</th>
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</tr>
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<td>.84</td>
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TABLE 5. Niche overlap. Computed using Horn's (1966) formula, where $R_{max}=1$, and $R_{min}=0$.

<table>
<thead>
<tr>
<th>Species/sex</th>
<th>Live vs. dead</th>
<th>Limb dia.</th>
<th>Foraging behavior</th>
<th>Foraging orient</th>
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<td>.84</td>
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DISCUSSION

The purpose of this portion of the study is to clarify the means by which the five scansorial species effectively segregate their foraging to avoid competition. A review of the data reveals a number of significant differences between the species. Investigations into other areas of behavior, reproduction and ecology would undoubtedly result in many other means of niche separation.

It appears that each of the birds shows a large degree of separation with the others along at least one resource dimension. For example, the condition of the substrate (live vs. dead) appears most significant for the Pileated Woodpecker. Its preferential use of subsurface feeding on dead substrate, within a large foraging range, effectively separates it from the other birds. This emphasizes the need for forest management which leaves dead trees in place rather than removing them.

The Brown Creeper is a scaling specialist, as shown in the niche breadth for foraging behavior. Its efficiency of movement along the bark surface allows for it to cover large areas of substrate in search for food. As will be discussed later, this scaling is partly related to the bill modification for access to cracks and
crevices.

The White-breasted Nuthatch exhibits a spatial separation within the same general habitat by utilizing both the undersides of limbs and the unique head-down locomotion. This movement provides access to a largely unexploited micro-habitat within the bark. The head-down position in particular likely orients the bird to items unseen from another viewpoint.

The congeneric Huttall's and Downy Woodpeckers showed the greatest degree of similarity, as might be expected due to similar morphologies.

Differences between the sexes of the Woodpeckers was, contrary to other published reports, minimal. Though sexual dimorphism is generally a sign of competition (Johnson 1966), the foraging behavior I observed can possibly be explained within the context of the season and food availability. As animals can be more selective in their food choices when food is abundant (Emlen 1966), greater overlap in foraging parameters during the spring may represent a common selectivity.

Those birds that appear superficially to be competing for the same resources are actually foraging in significantly different ways. This is reflected in the spatial separation of the birds to different micro-habitats within the bark substrate. This spatial separation can be either on the bark surface or in different levels within the bark surface. Different
morphologies reflect the functional ability of each species to access these micro-habitats. Specific adaptations will be discussed in Part 2.
PART II

FUNCTIONAL MORPHOLOGICAL ADAPTATIONS TO BARK FORAGING
ADAPTATIONS TO A SCANSORIAL, BARK FORAGING HABIT

The birds under investigation have evolved several functional adaptations which allow them to successfully access and exploit the bark substrate. Many characters are involved, with varying degrees of significance. It is the combination of all the physical and behavioral attributes which insures successful niche occupation.

For scansorial birds, anatomical adaptations exist in three primary categories, each specialized to a different degree. These three areas are: 1. climbing, 2. probing and 3. pecking. To a large degree, it is the amount of specialization within these three categories which effectively allows differential exploitation of food items within the feeding substrate.

CLIMBING

VERTICAL ORIENTATION

1. Stationary Forces

In order to successfully access the vertical bark surface as a feeding site, the bird must first be able to support its body weight against gravity in an energy efficient manner. An illustration of gravitational forces for a bird in a vertical position is shown in
Figure 6. This figure is adapted from Bock and Miller (1959). Here, the downward gravitational force is directed into two components. The first component, $a$, is directed outward from the point of attachment through the center of gravity, $c$, and tends to pull the bird off the substrate. This force is effectively countered by the laterally directed fourth toes (Spring 1965).

Additionally, the claws can be anchored into the wood for added support. For woodpeckers, the contraction of the flexor muscles around the joints of the last phalanges causes the claws to rotate and penetrate the bark surface (Dorst 1974).

The second component, $b$, is directed downward and towards the bark surface from the center of gravity. This is countered by both the anteriorly directed toes and, to a greater extent, by the stiff tail (Spring 1965). The posteriorly directed toes are believed to be insignificant for woodpeckers climbing on vertical surfaces (Dorst 1974, Schranke 1930, Stolpe 1932). I suggest that this toe may have a secondary function in helping to anchor the bird by attachment of the claw. A reduction or loss of the posteriorly directed hallux is believed to be a modification to delivering harder blows, by release from restrictions of heel movement (Spring 1965).

The posteriorly directed rami on the tail feathers add to the support capabilities of the tail
FIGURE 6. The gravitational forces on a vertically oriented bird. The center of gravity is indicated by C, while dashed lines a and b are force vectors. The effective countering gravitational vectors are shown by the dotted lines.

FIGURE 7. The right foot of a woodpecker. This perspective shows the lateral rotation of the fourth toe.
Marshall 1960, Norberg 1931). Of the birds under investigation, all but the White-breasted Nuthatch use the tail for support. This bird uses a separate and wide foot placement, in conjunction with a long tibiotarsus (Norberg 1970) to counter vector b. Essentially, this lower limb serves the same purpose as the tail in the woodpeckers, while having the added advantage of the gripping forces of the sharply curved claws.

Three important adaptations in the woodpeckers, which allow for effective opposition to gravitational vector b are: 1. the enlargement of the pygostyle; 2. tail feather morphology; and 3. foot morphology. An enlarged pygostyle, in relation to other less arboreal species has been reported by many observers (Shufeldt 1900, Burt 1930, Spring 1965). As the pygostyle is the location of musculature attachment of the tail feathers, and must support strong gravitational, climbing and pecking forces, adaptive modification is strongly evidenced in this area. Burt (1930) found that a relative increase in the size of the pygostyle disc, with a corresponding decrease in the length of the spine, was positively correlated with a greater arboreal habit. The broader pygostyle essentially increases the surface area of muscular attachment.

Feather morphology also plays an important role in countering gravity. Most scansorial birds possess long, stiff tail feathers with posteriorly directed rami,
which help to counter the effecting forces. These modifications then allow the tail to be used as both a prop and stabilizer for scansorial movement.

The third important adaptation to an arboreal habit is in the foot morphology. As described above, both anterior and lateral directing of toes is required for opposition of gravitational forces. In addition, the arboreal birds possess long curved claws which aid in clinging to the bark surface. These claws possess a much greater curvature than those of non-climbing birds. They can both pierce the bark surface when gripping, and then lock in place through contraction of the flexor muscles (Dorst 1974).

Most woodpeckers are able to rotate the fourth toe to a laterally oriented position when on a vertical surface (Figure 7). Lengthening of this toe may be an adaptation for climbing (Storer 1960). As mentioned earlier, the posteriorly directed hallux, or first toe, is believed not to be a factor for support and can actually impair heel movement during blow delivery (Spring 1965). This is surely the case in the Black-backed Three-toed Woodpecker (Picoides arcticus) which has lost the hallux, and obtains 85% of its food from pecking (Burt 1930).

This conclusion supports the theory that the zygodactyl orientation is not a modification for climbing or pecking, but is more of a perching foot (Bock and
Miller 1959). Numerous observers have noted that most woodpeckers rotate the fourth to a zygodactylous orientation while perching. This is perhaps an adaptation to perching because of the lack of the true "perching type" foot and locking mechanisms of the Passeriformes.

Neither the Brown Creeper, nor the White-breasted Nuthatch are able to rotate the fourth toe. Both, however possess the sharply curved claws. In particular, the nuthatches have a much larger claw on the hallux than on the other three toes (Storer 1960). Perhaps as a behavioral adaptation, I have observed the Brown Creeper, to take a broader stance while resting on the tree surface; separating the foot placement at an oblique angle. This puts the fourth toe in a naturally lateral position without rotation, creating greater stability while stationary. It is also possible that the creeper's significantly lighter weight and sharply curved claws partially compensate for any difficulty.

2. Climbing Forces

With the bird sufficiently anchored to the vertical bark surface, the next area of interest is the mechanics of vertical climbing. As discussed earlier, the tail is an integral part in upward movement. The tail feathers must act as a prop for support during foot movement and placement in vertical progression. Spring
(1965) found two types of tail action in his studies using a high speed camera. The first action involved continuous contact of the tail on the trunk, while in the second the tail left the trunk during the later part of the climbing cycle. These are related to the inward hitching movement of the bird during the first phase of upward movement. By bringing the body closer to the bark surface, there is a reduction in the outward vector of gravitational force, requiring less muscular work to move straight up. In birds which can hitch their bodies close to the trunk surface, continuous tail contact is most efficient. For those which hitch partially or not at all, the outward gravitational vector can be countered during the latter part of the climbing cycle by the outward flipping of the tail (Spring 1965).

Of the birds in this study, all but the Nuthatch used the tail as a continuous support unit during climbing. Additionally, all but the Nuthatch moved their feet synchronously in a single hop during vertical progression. In hopping, it should be noted that maximum efficiency is attained when foot placement is close together. This in effect puts the muscles more in line with the line of progression than if they were angled obliquely.

Instead of hopping, the Nuthatch walks with alternating leg movements (Norberg, 1981). The tail is not in direct contact with the bark surface, and
gravitational forces are countered by this foot separation acting to increase the base-line between the two contact points. Relative lengthening of the tibiotarsus by approximately 20% (Norberg, 1981) further increases this distance of support. It is possible that the lack of tail contact is necessary for the Nuthatch to move headfirst downwards on the bark surface, as tail use would be counter-productive to movement in this direction.

Additionally, the length of the leg bones may be functional in climbing ability. Specifically, a shortening of the tarsometatarsus would move the bird's center of gravity closer to the bark surface, reducing the outward gravitational vector.

OBLIQUE, BACK-DOWN, AND HEAD-DOWN ORIENTATION

1. Oblique Orientation

The preceding discussion dealt with movement on a vertical surface only. Oblique, upward movements on the vertical surface appear to incorporate the same mechanics, the difference being in the angle of tail support. My observations are that most oblique movements are accompanied by vertical movements, with the oblique direction a result of either an angling of the tail in the power stroke, and/or a movement of the upper body while hopping. The Nuthatch doesn't appear to follow
this pattern; using it's walking motion to direct itself.

Since all trees are not built straight up and down, various branching patterns, especially among the oaks, provide for an infinite number of angles potentially to be transversed. Horizontal movement along the top of the branch surface requires no special adaptations, with the woodpeckers often rotating the fourth toe to a position opposing the second and third; a position similar to the permanently zygodactylous ground woodpeckers (Spring 1965). Movement may then progress with or without the use of the tail. As the bird begins to move laterally away from the top of the branch, changing gravitational vectors result in changing forces on the musculature; the magnitude and direction depending on the distance from the center axis, and the diameter of the branch. Some lateral movements may be made with the bird remaining parallel to the center axis, with the lower foot used as a prop along the down side of the branch, and the upper foot used to grasp at the top surface of the branch. Further movement down the side of the branch may require the use of the tail as either a prop or counter-balance, and orientation of the bird perpendicular to the center axis.
2. Back-down Orientation

Orientation on the underside of horizontal branches provides a new set of problems (Figure 10). Gravitational components are now directed from the point of attachment through the center of gravity in a similar manner as vertical orientation. The downward vector, however, is not directed through the tail, and must be countered by the gripping forces of the toes. The tail may contribute some, however, through frictional forces to help prevent the center of gravity from moving directly under the point of attachment. A broad stance may be more efficient in this case by moving the center of gravity closer to the bark surface. It also optimizes the use of countering forces by the lateral toes.

Weight is undoubtedly a factor in this type of movement also, as there are likely structural and myological efficiency limitations to support capabilities. Hitching of the body inward during this movement is also an important factor, as tail support during foot placement is minimal. The walking locomotion of the Nuthatch is more suited to this movement as there is always a point of contact on the bark surface.

3. Head-down Orientation

The head-down orientation is one which is very
FIGURE 8. Gravitational forces on a back-down oriented bird. The center of gravity is C, the dashed lines a and b are the gravitational vectors, and the dotted lines are the effective countering forces.

FIGURE 9. Gravitational forces on a head-down oriented bird. The center of gravity is C, and the dashed lines show the uncountered gravitational vectors.
seldom used by any of the birds other than the White-breasted Nuthatch. The basic structural design of the woodpeckers and the creeper that makes them very suitable for vertical movement makes them very inefficient for a head-down progression. Specifically, the parallel placement of the feet in these birds requires that a gravitational vector be directed through a point below the foot attachment. Figure 9 shows the gravitational components in effect in this position. Essentially, the center of gravity would be rotated around the point of attachment (feet), and without a countering support, the birds bill and head would become one with the bark surface. The nuthatch, by virtue of its wide foot placement (Figure 10), uses the downward foot, set below its center of gravity, in conjunction with the posteriorly attached foot to prevent a concussion.

PROBING

Probing for food in itself is not necessarily a specialized behavior. Surface food may be gathered by any bird encountering it, so long as it meets certain size and diet requirements. Subsurface feeding becomes more of a problem, however, as insects and other food items may reside or retract to deep within the bark surface. In response, bark-foraging birds have evolved special bill or tongue adaptations to better access these.
FIGURE 10. The gravitational forces acting on a White-breasted Nuthatch in a head-down position. This shows the importance of the posterior foot placement. The center of gravity is C, the dashed lines the gravitational vectors, and the dotted lines the effective counteracting vectors.
areas.

The woodpeckers in particular have a specialized tongue mechanism which allows them to reach much further than their bill. This long, protrusible tongue is supported by hyoid bones which extend around the back of the skull, usually attaching near the base of the upper mandible (Perrins and Harrison 1979). An extreme example of tongue length can be found in the Green Woodpecker (*Picus viridus*) whose tongue length is four times the length of the upper mandible (Terres 1980). The ant-eating Northern Flicker also has a very long tongue. The length of the hyoid apparatus varies greatly between species, with corresponding different points of attachment. For example, in the Downy Woodpecker, the hyoidean extension "does not proceed further forward than opposite to the center of the eye" (Shufeldt 1930). Attachment of the hyoids to associated musculature allows for the tongue to be moved rapidly in and out, as well as side to side and up and down (Burt 1930). The hyoid apparatus of the creeper and nuthatch is much shorter than in any of the woodpeckers.

Another adaptation of the tongue other than its length, is in the morphology of its tip. A variation in shape exists between most bird families, which may be dependent on the birds' primary food resources (Terres 1980), or adapted to the feeding habit (Van Tyne 1976). The woodpeckers that feed on insects usually have a
tongue that is barbed, and coated with a sticky saliva from glands on the floor of the mouth (Dorst 1971), while the sapsuckers which feed on tree sap have tips with brushy hairs (Terres 1980). Nuthatches, by contrast have tongues with small fork-like projections at the tip (Terres 1980).

PECKING

The third important adaptation of bark-foraging birds, and perhaps the most osteologically specialized area is that related to pecking. All of the birds studied used the pecking behavior to one degree or another. In fact, in some species, pecking seems inadequate to describe the intense activity observed. While variations and adaptations in climbing ability can spatially orient the bird to different locations on the bark surface, any sub-cambial and some inner-bark food retrieval requires specialized pecking motions. Pecking use varied significantly within the bark foraging birds in both relative amounts and magnitude. These differences likely reflect the type of food items encountered and taken.

1. Head and Skull Adaptations.

Modifications to the head and skull in
woodpeckers have been discussed by many authors. (Shufeldt 1900, Burt 1930, Bock 1964, Spring 1965, May, et al. 1976, and others). As some woodpeckers repeatedly strike the tree surface with great force, structural characters must be present which eliminate head and brain injury, while retaining maximum blow efficiency.

Beginning with the bill, Burt found that those birds with a greater pecking and drilling habit showed:
1. a relative widening at the base of the premaxillae; 2. a shifting of the narial openings to a more lateral position; and 3. a straight rather than curved premaxillae. Both Burt and Spring found that an increase in pecking habits was associated with a decrease in the cranio-facial angle, with an eventual folding of the frontal bones over the base of the upper mandible. Spring found this extension of the frontal bones to be composed of a bony web of varying densities. Other modifications of the skull found to correlate with a greater pecking habit are: 1. a wider and larger brain case; 2. a thick interorbital septum; 3. a concave-anterior frontal/premaxillae angle; 4. a decrease in the angle of cranial kinesis; 5. increase in the relative size of the M. protractor quadrati and M. protractor pterygoidei; and 6. a more anterior positioning of the foramen magnum.

In all cases, adaptations appear to be related to either greater efficiency of blow force, functional
cranial buffering, or reduction of structural stress during concussion.

2. Leg Structure Modification

Variations in the relative lengths of the femur, tibiotarsus and tarsometatarsus were found by Spring (1965) to be significant to the magnitude of blow delivery. In his study, a relative reduction in the length of the distal leg bones was thought to be a modification for harder blow delivery. Further, increased efficiency in blow delivery was thought to be inversely correlated with climbing ability. Norberg (1981) reported that short legs are more efficient for climbing by placing the bird's center of gravity closer to the bark surface. Burt (1930) mentioned no such correlation, reporting little variability in the leg bones.

3. Neural Spine Modification

Spring (1965) found a significant variation in the spatial separation of the four thoracic vertebrae. A greater degree of separation allows for a larger amount of back flexion during blow delivery. Since more momentum is generated through use of the body during force generation than is produced through neck flexion, direct blow force can thus be increased.
ANALYSIS OF SELECTED ADAPTATIONS

In comparing birds of different families or orders, caution is necessary in making generalizations or summations. Similar morphologies may reflect different usage and different morphologies may accomplish the same function. However, since the physical laws of nature are preserved for all species, some direct comparisons can be made for certain characters.

Within the scope of this paper, I have chosen to analyze a limited number of characters. The choice of these characters was made from a review of the literature (as summarized in the previous section), and the accessability of available data. The discussion of the characters will be divided into three categories: 1. climbing; 2. probing and; 3. pecking.

Measurements of selected characters are listed in Table 6. Sources for this information are Ridgway (1904 and 1914), Burt (1930), Willson (1970) and measurements made by me. Specifics are included with the tables. Ratios are listed in Table 7.

CLIMBING

1. Leg structure

As related earlier, each of the species studied
TABLE 6. Anatomical measurements. Length measurements are in millimeters. Weight is in grams.

<table>
<thead>
<tr>
<th>Species/sex</th>
<th>Total Length</th>
<th>Tail Length</th>
<th>Bill Length</th>
<th>Bill Width</th>
<th>Tarsus Length</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nuttall's male</td>
<td>173</td>
<td>63.8</td>
<td>20.8</td>
<td>8.2</td>
<td>18.4</td>
<td>37.5</td>
</tr>
<tr>
<td>female</td>
<td>169</td>
<td>63.8</td>
<td>19.3</td>
<td>8.2d</td>
<td>17.9</td>
<td>37.5</td>
</tr>
<tr>
<td>Downy male</td>
<td>153</td>
<td>55.8</td>
<td>16.4</td>
<td>7.4</td>
<td>16.0</td>
<td>27.6</td>
</tr>
<tr>
<td>female</td>
<td>153</td>
<td>56.4</td>
<td>15.4</td>
<td>7.2b</td>
<td>15.4</td>
<td>27.6</td>
</tr>
<tr>
<td>Pileated male</td>
<td>410</td>
<td>152.9</td>
<td>49.7</td>
<td>18.6</td>
<td>34.1</td>
<td>368.0</td>
</tr>
<tr>
<td>female</td>
<td>390</td>
<td>149.4</td>
<td>44.9</td>
<td>18.6b</td>
<td>32.5</td>
<td>368.0</td>
</tr>
<tr>
<td>Brown Creeper</td>
<td>126</td>
<td>62.5</td>
<td>13.4</td>
<td>1.8c</td>
<td>15.1</td>
<td>8.2</td>
</tr>
<tr>
<td>White-breasted Nuthatch</td>
<td>131</td>
<td>46.8</td>
<td>18.6</td>
<td>3.9c</td>
<td>13.6</td>
<td>21.2</td>
</tr>
</tbody>
</table>

* Total length of the bird was measured from the tip of the bill to the tip of the tail.
  a. Ridgway (1904 and 1914).
  b. Burt (1930).
  d. SSU collection.
  e. Terres (1930).

The above measurements are all sample means. Sample size was unspecified for most data. Sample size, when given, ranged from 3 to 19.
TABLE 7. Ratios of the length measurements of various structures in Table 6.

<table>
<thead>
<tr>
<th>Species/sex</th>
<th>Tail/TL</th>
<th>Tarsus/Tail</th>
<th>Bill width/Bill length</th>
<th>Tarsus/TL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nuttall's male</td>
<td>.368</td>
<td>.288</td>
<td>.416</td>
<td>.106</td>
</tr>
<tr>
<td>female</td>
<td>.373</td>
<td>.281</td>
<td></td>
<td>.106</td>
</tr>
<tr>
<td>Downy</td>
<td>.364</td>
<td>.287</td>
<td>.459</td>
<td>.105</td>
</tr>
<tr>
<td>male</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>female</td>
<td>.369</td>
<td>.273</td>
<td></td>
<td>.101</td>
</tr>
<tr>
<td>Pileated</td>
<td>.373</td>
<td>.223</td>
<td>.393</td>
<td>.83</td>
</tr>
<tr>
<td>male</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>female</td>
<td>.383</td>
<td>.218</td>
<td></td>
<td>.83</td>
</tr>
<tr>
<td>Brown Creeper</td>
<td>.496</td>
<td>.242</td>
<td>.134</td>
<td>.120</td>
</tr>
<tr>
<td>White-breasted Nuthatch</td>
<td>.357</td>
<td>.397</td>
<td>.210</td>
<td>.142</td>
</tr>
</tbody>
</table>

a. TL = total length of the bird; from the tip of the bill to the tip of the tail.
b. Bill ratios are for combined male-female.
uses the bark scaling motion to one degree or another. One of the key adaptations to this movement is the shortening of the leg-bones. In finches, the arboreal species have been found to have shorter legs than the ground feeding ones (Newton 1967). This shortening was greatest in the tarsometatarsus, and least in the femur. In woodpeckers, this decrease in length moves the birds center of gravity closer to the bark surface, thus reducing the outward gravitational vector, and allowing for more efficient upward movement. The Brown Creeper, shows a similar shortening of the tibiotarsus (Norberg 1981). As discussed earlier, the White-breasted Nuthatch utilizes a different strategy for accomplishing the same movement. Because of the increased length of its tibiotarsus, it can move up the tree surface in a walking motion, with the trailing foot serving the same function as the stiff tail prop of the woodpeckers and creeper.

Table 6 lists the length of the tarsometatarsus (tarsus) for each of the species studied. More telling are the ratios listed in Table 7. Here the tarsus is listed as a percentage of the bird's total length. The Pileated Woodpecker is then shown to have the shortest relative tarsus, and the White-breasted Nuthatch the longest. The Nuttall's and Downy woodpeckers, and the Brown Creeper were intermediate. As mentioned earlier, the nuthatch has a relative lengthening of the tarsus to allow for its scansorial locomotion.
From these ratios, no direct correlation was found between distal leg measurements and percent of scaling. Though the Pileated Woodpecker has a relatively shorter tarsus than any others, it scales considerably less. The correlation between a relatively short tarsus and scaling is more pronounced when compared with other birds which do not have this scansorial habit. For example, tarsus/total length ratios (listed as a percent of the total length) for some other birds are: Hutton's Vireo; 16.5, Townsend's Warbler; 14.5, Marsh Wren; 16.6, and Chestnut-backed Chickadee; 13.7 (Dawson 1921). It appears then that a shortened tarsus is an adaptation by these scansorial birds as a group, and that species variations may be related to other functional characteristics.

2. Weight

A relationship was found between the percent of scaling and the body weight. Newton (1967) found body weight to be more important than the leg-length/body weight ratio in the ability of finches to climb and hang.

In figure 11, the log of the gram weight of the species studied vs. the percent of scaling is graphed. This shows a negative exponential relationship between these two variables suggesting that body weight is limiting, possibly due to osteological and myological
FIGURE 11. Graph of the log of bird weight vs. scaling percent. This shows the negative correlation between the log of the weight (in grams) of the birds and their scaling percentage.
Scaling (percent) vs. log of weight (grams)

- BC
- WBN
- DW
- NW
- PW
efficiency, in movement against gravity. Greater efficiency in scaling would occur, given the same equipment, when gravitational force is minimized by a reduction in mass. Here the probable trade-off is between a low mass, preferable for scaling, and a greater mass more functional in blow force for pecking, which will be discussed later.

The ability of a bird to efficiently move in an orientation other than vertically, or horizontally on top of a branch, is again largely a function of weight, leg and tail structure and placement. All of the species studied but the nuthatch must move with a hopping motion in which both feet are temporarily off the substrate (Norberg, 1981, Spring 1965). Movement along the underside of a branch must then involve both a forward movement and a hitching movement to bring the body close to the surface during foot placement. Here again, those birds which are most efficient at scaling, through lighter weight and a short tarsometatarsus are those which can more efficiently use the limb undersides.

The amount of back-down scaling for all the study birds shows a positive correlation with lighter weight. This relationship holds for the nuthatch, which has the added advantage of always having one foot in contact with the surface during movement.

Utilization of the head-down movement is limited almost solely to the white-breasted Nuthatch. The
hopping motion of the woodpeckers and creeper would be ineffectual in this movement as the tail could not provide any support in this orientation (Figure 9). In the Nuthatch, this movement (Table 3) would necessarily be done in very short increments, as an ended loss of contact with the substrate would result in rapid acceleration and difficulty in replanting the feet.

Complete analysis of foraging orientation is difficult because it depends largely on the form of the host trees. From my observations, a Brown Creeper feeding in an oak (which has extensive branching in varying angle gradations), uses the undersides more often than it would in a Douglas Fir, whose branches are lost at lower levels, and are horizontal or drooping at higher levels. Research involving the comparison of orientation on different vegetation types, and its effect on niche breadth and overlap would be enlightening in this area.

3. Length

An increase in the total length of the bird showed a negative relationship to the percentage of scaling also (Figure 12). It is probable that in this relationship, the length measurement is an indirect way of measuring the body weight, given a similar body shape, and may also reflect some optimum length ratios most favorable for scansorial movement. The tail length/total
FIGURE 12. Graph of the log of length vs. scaling percent. Length equals total length of the bird from the tip of the bill to the tip of the tail.
body length ratio is very similar for all birds except the Brown Creeper (Table 7). The greater similarity in the woodpeckers may correlate with an optimum bird to substrate distance and angle for support for climbing or at rest.

For the Brown Creeper, the tail comprises almost half the total length of the bird. One possible explanation for this is that in lacking the enlarged pygostyle necessary for maximum leverage in support, the longer tail provides more surface area for the supportive posteriorly directed rami.

PROBING

Probing is a difficult behavior to quantify, as it can be defined as taking any food item by a means other than pecking. This includes surface items that require no specialized features. Adaptive modifications for the woodpeckers are the extendable tongue, and the relatively thin bill tip. The Brown Creeper would appear to have the most specialized bill for probing because of its thin, curved shape which allows easy access to cracks and crevices. The bill of the White-breasted Nuthatch has a similar shape when viewed from above, but is deeper on the side with a straight to slightly upturned bill. Due to the phenoplasticity of the bill, changes in bill morphology may have been one of the first modifications expressed by these birds. Secondary anatomical
modifications to scaling, etc. may then have come later, with further refinements of bill function in response to new micro-habitats.

1. Bill Structure

The study of the relationships between bill morphology and feeding variables is common in the current literature. The bill is chosen as a trophic indicator largely because of its phenoplasticity; which is exhibited to a degree greater than any other single feature (Ashmole 1966). The positive correlation between bill size and body length is shown for the species studied in Figure 13.

Many researchers have studied the relationship between bill size and the size of food taken, often in conjunction with the dynamics of the foraging niche (for example; Kipfer and MacArthur 1961, Newton 1967, Schoener 1964, Willson 1971). Williams and Batzli (1979) related bill length to mean food size for some bark-foraging birds including the Downy Woodpecker, Brown Creeper, and White-breasted Nuthatch. They found that an increase in bill length was related to an increase in prey size. Abbott, et al (1977) in a study of Galapagos ground finches found those with larger beaks had more diverse diets. Schoener (1971) also suggested that the optimum prey size of the insectivorous birds studied was related to bill characters, but felt body size may be a better
FIGURE 13. Graph of the bill length vs. body length. This shows the positive relationship between the body length and bill length of the five study birds. Measurements are from Table 5.
indicator. Ashmole (1968) and Hespenheide (1971) felt that any one bill dimension was inadequate in defining foraging niche, citing the overuse of bill length as an indicator.

For those researchers who did relate bill size to prey size, most stressed food size as a function of bill length, with the birds with longer bills taking the larger food items. This can be significant in defining food niche breadth, and reducing niche overlap between sympatric, congeneric species. In this way food items can be partially segregated by size, thereby reducing competition for the similar resources.

Schoener (1965) found that large ratios of character difference (bill size) occurred among families who feed on food of relatively low abundance. He included the Picidae and Sittidae in this category. Apparently this could effect a more efficient use of the available resources by a greater specialization to food type, and reduce overlap with competing species.

For the bark-foraging birds under investigation, other factors come into play besides simple prey capture. Bills must be able to either access small crevices in the bark or widen inaccessible areas for bill or tongue penetration. For this reason the bill shape may be either specialized (such as to structural stability and rigidity for pecking, or lightness and thinness for speed and manipulation) or a compromise between two or more
functions. A bird which uses forceful blows to obtain subcambial food would need a bill with a broad base and medium length to optimize percussionary force at the tip (Johnson 1966). Prey size would then be limited by the size of the gape and the speed of manipulation. A bird which relies on probing of small cracks and crevices, or taking prey by surprise would need a long slender bill for ease and speed of angular manipulation. In this case prey size is limited by size of the gape and musculature of the bill closing mechanism; as the effective force at the tip of the bill is inversely proportional to its length (Ashmole 1963).

Lateral shape of the bill is also important, particularly in blow delivery. As woodpeckers deliver straight blows to the substrate (Spring 1965), maximum force would occur with a straight bill (Bock 1966). Curvature of the bill up or down would reduce the force at impact.

PECKING

1. Leg structure

Spring (1965) suggested that a shortening of the distal leg bones was a modification for the delivery of harder blows, though he was unclear as to the reason for this. Further, he felt that scaling ability was inversely related to harder blow delivery, though the magnitude was not quantified. My research can neither
confirm nor reject this theory, though the Pileated Woodpecker, which has the lowest tarsus/total body length ratio, also pecked more than the other species. It is probable that this shortened tarsus works in conjunction with other variables such as skull and bill structure, back and neck flexion, and weight.

2. Skull structure

Modifications of the skull and bill are two areas often studied in woodpeckers and other birds. Specifically, functional adaptations of the skull of Picidae are believed to provide buffering mechanisms for the brain to eliminate possible injury (May, et al. 1976). The actual mechanics of this buffering are still the topic of research. Enlightening information on bill percussionary forces can be found in Bock (1966). Analysis of cranial kinesis or kinetic buffering mechanisms was not attempted in my study.

Burt (1930) suggested that a decrease in the cranio-facial angle, with an eventual folding under of the frontals, provided greater strength and stability for pecking. Of the five birds in this study, only the two Picoides species show any folding under of the frontals, though they pecked less than the Pileated Woodpecker. The Brown Creeper and White-breasted Nuthatch have no such folding. Burt explains the difference in skull structure in the Pileated Woodpecker by noting its
behavioral preference for dead or decaying wood for feeding, which is softer and requires less force to excavate.

Gordon (1976) suggested that the general lack of pneumatisation in the skulls of the British woodpeckers and Sittidae species allowed stronger blows with less head injury.

Important myological modifications (which could not be measured in this study) include the large protractor quadrati and protractor pterygoidei muscles in woodpeckers (May, et al 1976) and the protractor quadrati in the nuthatches (Spring 1965).

3. Bill structure

Illustrations of the bills of the species studied are shown in Figure 14. Each is unique in shape. As predicted, the bird which pecks the least (the Brown Creeper) has the bill with the greatest curvature and the least bill width to bill length ratio (Table 7). This shape is indicative of the more manipulative bill shape which is more efficient in accessing small crevices in the bark surface.

The nuthatch bill is similar to the creeper from above, with the nuthatch bill showing some broadening at the base. It is likewise broader in profile. The three woodpeckers each show a broadening at the base of the bill for pecking stability and shock dispersion. Both the Downy and Nuttall's Woodpeckers show a straight and
Figure 14. Illustrations of the study birds' bills. This shows the top and side views. All drawings are x2 except for the Pileated which is x1.2. Bills were illustrated from skins in the Sonoma State University vertebrate collection.
DOWNY
\[x 2\]

NUTTALL'S
\[x 2\]

PILEATED
\[x 1.2\]
WHITE-BREASTED NUTHATCH x 2

BROWN CREEPER x 2
pointed side view, while the Pileated Woodpecker has broader sides near the tip. For the Pileated, this may provide greater strength for the frequently observed lateral blows used to widen crevices.

Table 6 lists the bill lengths and widths for the species studied. Bill ratios are found in Table 7. As in scaling, the amount and efficiency of pecking is related to different factors, many of which are discussed in the previous sections.

To consider the question of relationships between bill length, bill width and bird weight, I derived a formula for the percent pecking based on these three characteristics.

\[
\text{percent pecking} = \left( \frac{\text{bill width}}{\text{bill length}} \right) \left( \sqrt{\text{weight}} \right) \times c
\]

where the weight is in grams, and the constant, c, is 6.0. Comparisons of calculated and observed percentages are listed in Table 8.

This formula suggests that pecking efficiency is increased by a high bill width/bill length ratio (a broad base for stability) and greater body weight (higher mass, and inertia at impact).
TABLE 8. Pecking index. Length measurements are in millimeters. Weight is in grams.

\[
\text{(bill width/bill length)} \times \left(\sqrt{\text{weight}}\right) \times 6.0 = \% \text{ pecking}
\]

<table>
<thead>
<tr>
<th>Species</th>
<th>Observed</th>
<th>Calculated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nuttall's</td>
<td>13.0</td>
<td>15.4</td>
</tr>
<tr>
<td>Downy</td>
<td>15.6</td>
<td>14.5</td>
</tr>
<tr>
<td>Pileated</td>
<td>44.6</td>
<td>45.3</td>
</tr>
<tr>
<td>Brown Creeper</td>
<td>2.6</td>
<td>2.3</td>
</tr>
<tr>
<td>White-breasted Nuthatch</td>
<td>4.6</td>
<td>5.8</td>
</tr>
</tbody>
</table>
DISCUSSION

A review of this investigation suggests certain patterns in anatomical/behavioral adaptations. Scansorial bark-foraging birds as a whole show adaptations unique from non-scansorial birds. Leg, foot, skull and bill structures are some of the features showing varying degrees of adaptations.

For the species studied, it is apparent that the foraging specializations found in Part 1 are partially dependent on the weight of the bird and its total body length. Specifically, lighter and smaller birds appear to scale more and peck less. The amount of pecking is related to both the weight of the bird and the bill morphology. Increased pecking is positively correlated with increased weight, increased length, and a higher bill length/bill width ratio.

Gradations to these opposing specializations, in conjunction with other anatomical modifications, result in efficient functional diversity. Those features related to bill morphology are the most visually evident, and since they are most directly related to prey capture are likely to be the most specialized.

It is this combination of specialized attributes, which act in combination as a complex whole,
that allows the exploitation of differing segments of the environment. The relative importance of each character is difficult to determine, as each is related to some degree with others in the organism. An attempt has been made in this study to compare and quantify some of these characters to their observed behavior. It is through future investigations and comparisons of morphology and behavior, in different habitats and for different variables, that accurate models of this complex system may be made.
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APPENDIX 1

CHECKLIST AND STATUS OF THE BIRDS OF THE BOUVERIE AUDUBON PRESERVE

INTRODUCTION

This paper is a summary of the status and distribution, to date, of the birds at the Bouverie Audubon Preserve.

The following information comes from two primary sources. The actual checklist of species is almost entirely from my own field observations. A few sightings from qualified individuals are included. Habitat associations are from personal observations, confirmed with appropriate references. The Redwood Region Ornithological Society (RROS) publication of the "Birds of Sonoma County" (Bolander and Parmeter 1970) was helpful for seasonal distribution and breeding status.

Nomenclature of scientific names, and common names are from the American Ornithologists' Union 1983 checklist. For additional information on field marks, behavior etc., I recommend the National Geographic Society "Field Guide to the Birds of North America".

NOTATIONS

1. Abundance

   Common: almost certain to be found within the appropriate habitat(s).

   Uncommon: present, but not certain to be found within the appropriate habitat(s).

   Rare: only a few annual records, not seen daily.

2. Occurrence

   Resident: birds may be permanent, summer or winter residents. Summer residents usually occur mid-spring to late summer or fall. Winter residents arrive in late summer or fall and leave during the spring.

   Migrant: birds may be spring or fall migrants, usually passing through the area on their way to or from wintering grounds.

   Visitant: birds can be spring, summer, fall or winter visitants. These birds are within their normal range, but occur
only intermittently and are not migrants.

It should be noted that some variability will exist in occurrence and abundance, depending on yearly seasonal fluctuations, predation and other natural occurrences.

3. Habitat associations

Habitat associations, when listed by plant community, are defined in Munz and Keck "A California Flora" (1959). Note: A Bouverie Audubon Preserve map of plant communities has been produced, and should be accessible soon.

GR = Valley Grassland
OW = Northern Oak Woodland
RW = Riparian Woodland
ME = Mixed Evergreen Forest
CH = Chaparral
FM = Freshwater marsh

A = Aerial
RU = Rural

4. Breeding

+ symbol denotes that nesting is confirmed; either by seeing the bird building the nest, on the nest, or feeding the young.

* symbol denotes nesting likely; due to the time in residence or other historical data for the area, but is not confirmed.

- symbol denotes that nesting does not occur here.

? symbol denotes that breeding status is unknown.

THE BIRDS

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Abundance/occurrence</th>
<th>Habitat</th>
<th>Breeding</th>
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<td>Scientific Name</td>
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<td>Cathartes aura</td>
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<td>Species</td>
<td>Status</td>
<td>Distribution</td>
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<td>Location(s)</td>
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<td><em>Picoides nuttallii</em></td>
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**Contopus sordidulus**  
Olive-sided Flycatcher

**Contopus borealis**  
Violet-green Swallow Common summer resident  
*Tachycineta thalassina*

**Barn Swallow**  
*Hirundo rustica*  
Common summer resident  

**Cliff Swallow**  
*Hirundo pyrrhonota*  
Common summer resident  
RU, banks

**Steller's Jay**  
*Cyanocitta stelleri*  
Common perm. resident  

**Scrub Jay**  
*Aphelocoma coerulescens*  
Common perm. resident  

**Common Raven**  
*Corvus corax*  
Common perm. resident  
OW,A,MEF

**American Crow**  
*Corvus brachyrhynchos*  
Common perm. resident  
OW,RW,GR

**Chestnut-backed Chickadee**  
*Parus rufescens*  
Common perm. resident  
OW,RW,MEF  

**Plain Titmouse**  
*Parus inornatus*  
Common perm. resident  
OW,RW,MEF

**Bushtit**  
*Psaltriparus minimus*  
Common perm. resident  
OW,MEF,RU

**Brown Creeper**  
*Certhia americana*  
Common perm. resident  
OW,MEF,RU

**Wrentit**  
*Chamaea fasciata*  
Common perm. resident  
CH,RU

**White-breasted Nuthatch**  
*Sitta carolinensis*  
Common perm. resident  

**House Wren**  
*Troglodytes aedon*  
Common summer resident  
OW,RW,RU

**Winter Wren**  
*Troglodytes troglodytes*  
Uncommon winter resident  
RU

**Bewick's Wren**  
Common perm. resident  
OW,RW,RU
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<td><em>Thryomanes bewickii</em></td>
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<td>Species</td>
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<td>Loxia curvirostra</td>
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Rufous-sided Towhee *Cor:ton pern.* resident
*Pipilo erythrophthalmus*

Brown Towhee Common perm. resident
*Pipilo fuscus*

Lark Sparrow Uncommon perm. resident
*Chondestes grammacus*

Dark-eyed Junco Common perm. resident
*Junco hyemalis*

Chipping Sparrow Common summer resident
*Spizella pallida*

White-crowned Sparrow Uncommon winter resident
*Zonotrichia leucophrys*

Golden-crowned Sparrow Common winter resident
*Zonotrichia atricapilla*

Song Sparrow Uncommon perm. resident
*Melospiza melodia*
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