

NATURAL HISTORY OF THE NUTTALL WOODPECKER AT THE HASTINGS RESERVATION

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FOREWORD

Between 1954 and 1964, the late Alden H. Miller involved himself at irregular intervals in a field study of the Nuttall Woodpecker (*Dendrocopos nuttallii*) at the Hastings Natural History Reservation, Monterey County, California. I have attempted in this paper to present the results of this study, based upon Miller's partially analyzed data. I wish to thank John Davis for making available these data as well as pertinent field notes of other observers at the reservation. Among the latter, G. A. Bartholomew, H. Hjermsman, J. T. Marshall, Jr., and especially T. Riney made extensive observations of local *D. nuttallii*. John Davis kindly read and criticized the original manuscript. Gene M. Christman prepared the illustration (fig. 1).

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The Nuttall Woodpecker is one of a group of "ladder-backed" *Dendrocopos* species (Voous 1947), so-called because they exhibit transverse black and white barring dorsally. In North America there are three such species, similar in appearance and occupying closely complementary ranges. The Red-cockaded Woodpecker (*D. borealis*) inhabits pine forests of the southeastern United States (Bent 1939; Ligon 1970), occurring west to eastern Texas and Oklahoma (A.O.U. 1957). The Ladder-backed Woodpecker (*D. scalaris*) is most typical of desert scrub, ranging from Texas, Oklahoma, and southern Colorado to southeastern California and south through México and Central America to northeastern Nicaragua. *Dendrocopos nuttallii* is largely endemic to California, where it is common in mesic oak woodland and riparian situations (Bent 1939; Short, in press).

While the autecologies of many North American woodpeckers have been well studied (e.g., Howell 1952; Kilham 1958 and others;

Stickel 1965; Davis 1965; Lawrence 1967; Dennis 1969), the ladder-backed *Dendrocopos* species have received relatively less individual attention. Ligon (1970) has recently reported on a study of the Red-cockaded Woodpecker in Florida, while Short (in press) has studied the systematics, ecology, and behavior of *Dendrocopos* species, including the "ladder-backed" forms.

Root (1967:346) proposed the term "ecological 'guild' . . . for groups of species that exploit the same class of environmental resources in a similar way." He pointed out (p. 335) that "one advantage of the guild concept is that it focuses attention on all sympatric species involved in a competitive interaction, regardless of their taxonomic relationship." There is also value to recognizing and comparing species ecologies within truly taxonomic guilds, whether in sympatry or not. This calls attention to processes of adaptive radiation and the plasticity possible within a certain basic ecological pattern, or, in other words, to the existing variations on a phylogenetic theme. North American Picidae appear to be among the better known and easily recognized "taxonomic guilds," and we hope that this study will further an understanding of the group.

THE STUDY AREA

All field data were collected by means of direct observation of Nuttall Woodpeckers on the Hastings Reservation. The reservation lies between 1500 and 2750 ft elevation at the northern end of the Santa Lucia Mountains in Monterey County, California. Rainfall, which averages 22 inches annually, falls almost entirely between December and March, summers being hot and dry.

There are three general habitat types utilized by Nuttall Woodpeckers on the Hastings Reservation. North-facing slopes are covered by deciduous oak woodland, largely blue oak (*Quercus douglasii*) and valley oak (*Q. lobata*). Exposed south-facing slopes are covered with chaparral species, predominantly

TABLE 1. Plant species availability and utilization by foraging Nuttall Woodpeckers at the Hastings Reservation.

Plant species	Availability		Minutes of utilization							
			Total		April-June		July-Nov.		Dec.-March	
	n	%	n	%	n	%	n	%	n	%
Live oak (<i>Quercus agrifolia</i>)	71	26.0	779	39.54	33	11.34	322	36.67	424	52.93
Blue oak (<i>Quercus douglasii</i>)	68	24.9	504	25.58	191	65.63	80	9.11	233	29.09
Valley oak (<i>Quercus lobata</i>)	57	20.9	338	17.16	50	17.18	240	27.33	48	5.99
Oak subtotal	196	71.8	1621	82.28	274	94.16	642	73.11	705	88.01
Chamise (<i>Adenostoma fasciculatum</i>)	2	0.7	135	6.85	-	-	65	7.40	70	8.74
Willow (<i>Salix</i> spp.)	31	11.4	95	4.82	15	5.15	77	8.77	3	0.37
Sycamore (<i>Platanus racemosa</i>)	9	3.3	53	2.69	-	0	40	4.56	13	1.62
Elderberry (<i>Sambucus glauca</i>)	2	0.7	6	0.30	-	-	6	0.68	-	-
Poison oak (<i>Rhus diversiloba</i>)	2	0.7	3	0.15	-	0	1	0.11	2	0.25
Miscellaneous	31	11.4	57	3.00	2	0.69	47	5.46	8	1.00
Totals	273	100.0	1970	100.00	291	100.00	878	100.00	801	100.00

chamise (*Adenostoma fasciculatum*). Canyons and shaded areas support a mixed woodland, common species being live oak (*Quercus agrifolia*), western sycamore (*Platanus racemosa*), big-leaf maple (*Acer macrophyllum*), and California bay (*Umbellularia californica*). Important brushy species in moister areas include willows (*Salix* spp.) and cream bush (*Holodiscus discolor*). For a more complete description of the Hastings Reservation, see Linsdale (1943).

HABITAT UTILIZATION

GENERAL DISTRIBUTION AND HABITAT

According to the American Ornithologists' Union Checklist (1957), the Nuttall Woodpecker is "resident in California west of the deserts and the Sierra divide, from southern Humboldt and Sonoma counties and the head of the Sacramento Valley south to northwestern Baja California." Short (1965) has reviewed possible records of *D. nuttallii* in Oregon. It probably occurs there only very rarely.

Within its range the Nuttall Woodpecker most typically occurs in oak woodland. Miller (1951), in analyzing the distribution of the birds of California, lists "oak woodland" as the primary habitat of *Dendrocopos nuttallii* and "riparian woodland" as a secondary habitat. Bendire (1895) likewise found the species most abundant in oaks, but also in riparian cottonwoods (*Populus*), willows, sycamores, and the like. Where oaks are scarce, as in parts of southern California and Baja California, Nuttall Woodpeckers are most abundant in riparian situations (Grinnell and Miller

1944; Short, in press). Chaparral is utilized, but only where it is associated with larger trees which can serve as nest/roost sites. Most field observers agree that Nuttall Woodpeckers completely avoid pure coniferous forest (Belding 1878; Dawson 1923; Grinnell and Miller 1944), although Short (in press) found birds foraging in pinon pines (*Pinus cembroides*) in the San Bernardino Mountains of southern California.

HABITAT UTILIZATION AT THE HASTINGS RESERVATION

Table 1 is a summary of plant species utilized by Nuttall Woodpeckers at the Hastings Reservation, based upon 1970 minutes of direct observation of foraging birds. These data are divided into three periods: the breeding season (April-June); the post-breeding dry season (July-November); and the wet season (December-March). Included in table 1 are data on tree availability, based upon a strip census through the reservation about 100 yards wide and 0.5 mile long. Brushy species were counted as "clumps" 30-50 ft across the crown, rather than on the basis of trunks, in an attempt to make tree and brush "individuals" equivalent.

From table 1, it is obvious that oaks are the mainstay for foraging Nuttall Woodpeckers at the Hastings Reservation, both in terms of availability (71.8%) and selection (82.3%). However, there are important seasonal shifts

TABLE 2. Nest tree preference of Nuttall Woodpeckers, based upon literature references, unpublished field notes, and personal observations.

Nest trees	n	%
Willow	11	19.3
Sycamore	10	17.5
Cottonwood	9	15.8
Alder	7	12.3
Valley Oak	4	22.8
Live Oak	2	
Blue Oak	1	
Oak sp.	6	
Elderberry	2	3.5
Laurel	2	3.5
Fencepost	2	3.5
Maple	1	1.8
Total	57	100.0

in oak utilization. During the breeding season when deciduous species are newly leafed-out, birds foraged almost exclusively in oaks, particularly in the blue oak (table 1). This species occurs in nearly pure stands on certain north-facing slopes; individual woodpeckers often ranged for hours, foraging particularly on and around branchlets and leaves of the blue oaks. At other times of the year, Nuttall Woodpeckers foraged predominantly in live oaks (table 1), especially during the winter and early spring when other trees are bare. The woodpeckers spent less time feeding in oaks during the summer and fall than in other seasons. This is probably due to the availability at this time of seeds and fruits of other sorts of riparian and chaparral plants. Even during the summer season, however, *Dendrocopos nuttallii* continued to utilize oaks approximately in proportion to their availability (table 1).

NEST SITES

Short (in press) found Nuttall Woodpeckers in southern California nesting in willows, cottonwoods, and sycamores. At Hastings Reservation, *Dendrocopos nuttallii* usually nested in sycamores or willows. Table 2 is a summary of literature references, unpublished field notes, and personal observations of nests from throughout the species' range in California. While birds occasionally nest in oaks, they seem to prefer soft-wooded species (table 2). This probably relates to the fact that the Nuttall Woodpecker is not specialized to chisel into wood for insect food, but is more of a surface gleaner and probing species (see "Feeding Ecology"). In 45 of 48 recorded cases, nest

sites were in dead trunks or limbs, indicating again the preference for soft wood.

The following data on nests were taken from the sources mentioned above: nest heights, 3-45 ft ($\bar{x} = 17$; $n = 54$); hole diameter, 1.5-3 inches ($\bar{x} = 2$; $n = 6$); cavity depth 5-18 in ($\bar{x} = 11$; $n = 12$).

CONCLUSIONS

W. L. Dawson (1923) noted that it was easiest to predict where *Dendrocopos nuttallii* would not be found (e.g., pine forest), but that the most likely place to find the species is where riparian vegetation is bordered by or mixed with oaks. We have found that Nuttall Woodpeckers prefer oaks for foraging and riparian trees for nesting, which would make the situation described by Dawson ideal habitat for the species.

FEEDING ECOLOGY

FOODS

The foods that Nuttall Woodpeckers consume are not seen readily at the time they are eaten. The specific items that we have noted are mainly berries and fruits, but only because these can easily be identified as the woodpeckers work on them. Many hours of watching show that most of the effort is directed toward search for surface or subsurface insects in places where little or no edible plant material would be found (table 1). Our experience in watching foraging is then fully in accord with Beal's conclusion (1911), based upon analysis of the contents of 53 stomachs, that about 80% of the food is animal matter. Much dependence must be placed on Beal's original studies of the food habits of this species; only a few specific items have since been added to the record.

Vegetable material. Fruit amounted to 8.49% in Beal's analysis and was present in 15 individuals taken in summer and fall months; there was one occurrence in December. Fruits of *Rubus* were found in two instances, but the principal fruit he detected was elderberry (*Sambucus*), a food source widely present in the range of the Nuttall Woodpecker. The seeds or berries of poison oak (*Rhus diversiloba*) appear in the record often enough to indicate that they are sought and taken regularly.

In a species that is confined very largely to oak woodland, it is strange that little attention is given acorns. We have never seen Nuttall Woodpeckers pounding on acorns and they do not seem to be attracted by the stores of the Acorn Woodpecker (*Melanerpes formicivorus*) even though they commonly work over

the limbs of the storage trees of that species. However, Beal did report acorn mast in five stomachs and this combined with poison oak seeds largely accounted for the 12% of vegetable material other than fruit.

Emlen (1937) reported Nuttall Woodpeckers taking almonds at Davis, Solano County, California. Bock (1970) found *Dendrocopos nuttallii* attempting to rob the winter almond stores of Lewis Woodpeckers (*Asyndesmus lewis*) in the Livermore Valley, Alameda County, California.

Nuttall Woodpeckers occasionally take sap, but never, so far as we know, develop a series of holes especially for this purpose as do sapsuckers (*Sphyrapicus*). On 21 October, a series of sapsucker holes had been made and were being used by a Yellow-bellied Sapsucker (*S. varius*) in a non-native birch at Hastings Reservation. Members of a pair of Nuttall Woodpeckers visited the sap workings and lapped up sap repeatedly. The sapsucker was dominant over the woodpeckers and drove them away on several occasions. On 10 July, an independent juvenile Nuttall Woodpecker spent half an hour feeding from sap oozes in a red willow (*Salix laevigata*) at the reservation. Apparently there was an old injury which the woodpecker had developed by fresh pecking. The hole was not shaped as in sapsucker workings but consisted merely of an enlargement of a bark break that may have resulted from earlier rubbing together of the limbs. There are no sapsuckers in the area at this season and it was evident that the Nuttall Woodpecker had torn away some cambium. There was a continual flow of sap so that a drop reappeared every 5 sec.

Animal material. All identified items in this category consisted of arthropods, and the beetles alone constituted 28% of the total diet reported in Beal's analysis. Larvae of the Cerambycidae and Elateridae were the most prominent elements. The first of these are wood borers in the larval stage and their presence reflects the work of the woodpeckers in penetration of the bark of woody plants. Larval elaterids (click-beetles) may also occur in rotten wood and it probably is here rather than in the ground that Nuttall Woodpeckers take them. Beal recorded considerable numbers of small leaf beetles (Chrysomelidae) and surmised that these were taken from leaf surfaces; this seems highly probable in view of the extensive leaf scanning that we have seen the birds carry on. Beal also found weevils of the genus *Balaninus* that feed on acorns, a type of prey likely to be encountered in the

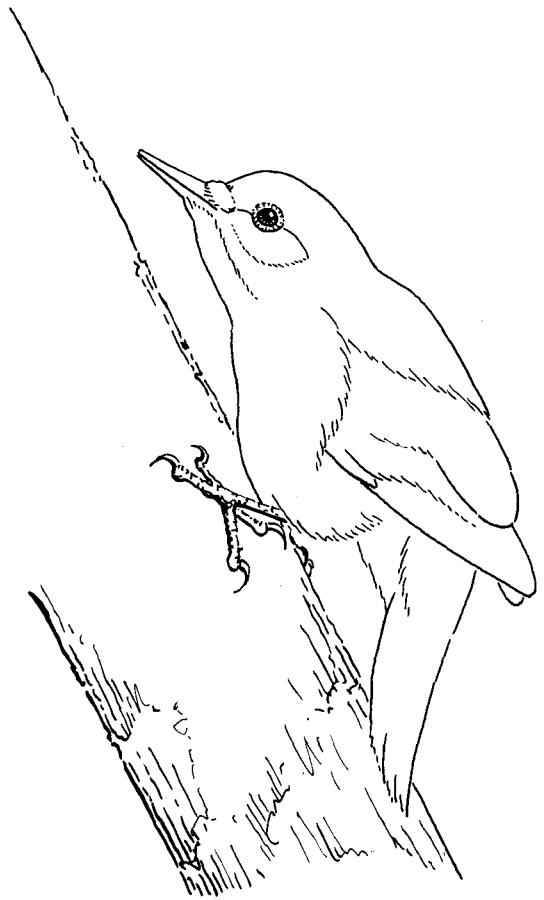


FIGURE 1. Foraging posture of a Nuttall Woodpecker gleaning for surface and subsurface insects.

oaks in which Nuttall Woodpeckers spend much time (table 1).

Hemipterans follow beetles as the second largest animal food category (14.7% of all food). They probably are all taken on the surface or in the foliage, as are most of the lepidopterous caterpillars that constituted the third major animal food category (14.2% of all food). Ants are not much favored as food in comparison with the degree to which they are utilized by some other woodpeckers, notably flickers (Beal 1911). They constituted but 8% of the food in Beal's samples.

FORAGING METHODS AND TYPES

Nuttall Woodpeckers possess the basic equipment of tail and feet common to woodpeckers which permits scansorial activity, in more or less vertical posture, on tree trunks and branches (see W. Bock and Miller 1959; Spring 1965). However, the species uses this stereotyped trunk climbing movement much less than its congeners, the Hairy (*Dendrocopos villosus*) and Downy Woodpeckers (*D. pubescens*), and in turn is more versatile and

acrobatic. This difference may arise in part from the tangled, irregular growth form of the tree branches and chaparral which the Nuttall Woodpecker frequents. On the other hand, the two other species, when foraging in these same plant formations at the Hastings Reservation, showed less of this diversified activity.

This diversity of foraging behavior is typified by the following deviations from the usual woodpecker program of upward hitching along a surface, with the bill more or less horizontally directed at right angles to the surface: (1) the woodpeckers seldom moved more than a foot or so without circling or working on another aspect of the trunk or branch; (2) they frequently hopped across to adjoining surfaces of nearby limbs or trunks; (3) they often almost crept rather than hitched along a foraging surface, assuming a rather humped posture, with the bill thrust ahead or somewhat tangentially (fig. 1); (4) bark scaling and probing were much more common than horizontal, right-angle tapping; (5) birds hopped freely into tangles of $\frac{1}{4}$ -inch twigs, using the tail not at all or only when an opposing surface happened to be available; (6) scanning surrounding leaf and twig clusters for surface insects occurred frequently; (7) birds often hopped into small limbs and perched crosswise, with the tail thrust ventrally but not in contact, as a balancer; (8) they crept through foliage masses with no more than $\frac{1}{8}$ -inch twig support, fluttering and balancing with the wings; (9) they gathered fruits while climbing in foliage clusters or while hanging upside down, with or without a tail brace; and (10) they occasionally pursued insects in the air, tumbling out from or down through the foliage in the process.

This multiplicity of foraging methods defied classification or quantitative appraisal, for the shifts from one type to another or back to normal woodpecker stance were complex and highly irregular. Opportunism in food sources and response to local tree or brush configuration, itself irregular, appear to dictate the next move. Of the various foraging techniques employed, trunk and limb gleaning and probing and foliage and twig scanning were seen more frequently than actual excavation or flycatching or sapsucking.

Short (in press) observed similar foraging behavior in *Dendrocopos nuttallii* in southern California and noted that the Ladder-backed Woodpecker (*D. scalaris*) used an identical foraging repertoire.

Although true excavation is considered a more "typical" woodpecker foraging tech-

nique, superficial probing, gleaning, and scanning are in fact common in many woodpeckers, including other *Dendrocopos* (Short, in press), the Lewis Woodpecker (Bock 1970), and *Centurus* species (Selander 1966). The ladder-backed *Dendrocopos* species appear unusual only insofar as they have minimized subsurface excavation as a foraging technique in comparison with other members of the genus.

THE ANNUAL CYCLE

DENSITY AND TERRITORIALITY

Lawrence (1967) distinguished between a woodpecker "territory," a small area near the nest defended against all intruders regardless of species, and a more flexible "range," whose boundaries are not precise and which is defended only intraspecifically. Nuttall Woodpeckers aggressively protect their nest sites against many species (see "Interspecific Competition and Aggression"); in addition, permanent pairs occupy year-round "ranges."

Figure 2 shows the ranges of seven pairs of *Dendrocopos nuttallii* as occupied October 1954–July 1955 on the Hastings Reservation. The boundaries are only approximations since the birds usually foraged in the central portions of their ranges. However, it is apparent that the pairs centered their activities along drainage patterns where both oaks and softwooded trees were available, each pair occupying an area approximately 0.5 miles along a stream bed. Only four conflicts, all involving males, were observed during 2800 bird-min of observation in 1954–55; each occurred at or near a range boundary (fig. 2).

A summary of all field observations at the Hastings Reservation indicates that most aggression between adult males occurs during the breeding season in the spring (table 3). The lack of encounters observed during April probably is due to the fact that the males are occupied with nest excavation and/or incubation at this time and are not moving about much on their ranges. Encounters between two males usually were preceded by a period of drumming back and forth across a range boundary. The birds would then approach and exchange loud, aggressive rattling and sucking calls, accompanied by displays involving crest elevation, bill-pointing, and wing extension and flicking similar to aggressive movements described for other *Dendrocopos* species (Lawrence 1967; Kilham 1969; Short, in press). Actual overt attack or at least chasing usually followed.

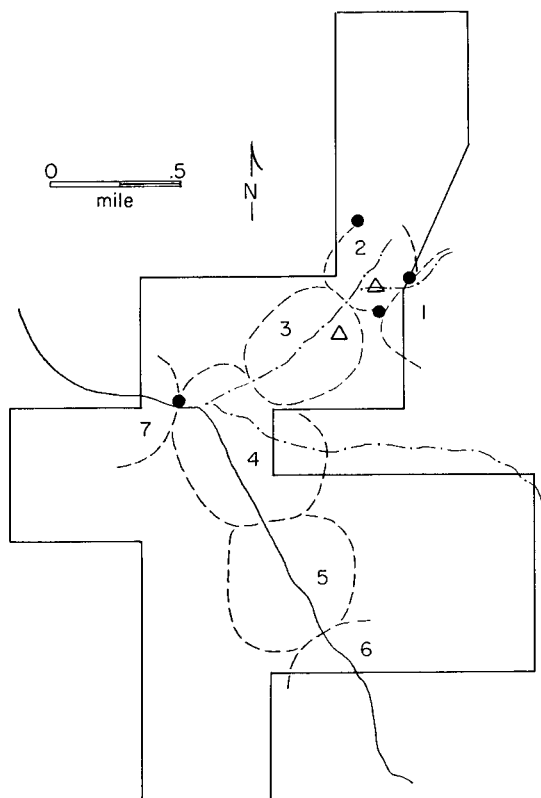


FIGURE 2. Map of the Hastings Reservation, showing the locations of Nuttall Woodpecker ranges in 1954-55. Dots represent the locations of observed aggressive encounters between males; dashed lines indicate approximate range boundaries; triangles represent nest sites. Note that ranges occur along drainages and appear to be roughly 0.5 miles across.

Encounters between female Nuttall Woodpeckers were rare (table 3), and no male-female encounters were observed except, obviously, between members of the same pair. On 16 April 1956, Miller recorded the following interaction, which began with two females drumming about 50 ft apart:

"Second female drums again and female number one gives a loud sucking aggression note. Female two comes to the tree of female one, alighting below about 15 feet, and moves up to within 10 feet; sucking notes of loud type follow. Female two holds rigid with bill pointed straight up at other bird. Female one remains at drumming station and both freeze on guard, silently, for two minutes. Female two raises and spreads both wings, giving sucking notes, and moves up into small branches; female one flies off down through the oaks 150 feet to the north."

Another sort of "territorial" aggression occurs in late summer when adults become intolerant of juveniles. Fledged young birds often were seen following adults and giving begging "trill" notes. Such behavior was common in early July 1955, but by the first week of August the trilling had ceased and an adult

TABLE 3. Aggressive encounters between Nuttall Woodpeckers at the Hastings Reservation.

Type of encounter	Month												
	J	F	M	A	M	J	J	A	S	O	N	D	
Male × male	1	1	7		6						1	1	1
Female × female		1		1									
Adult × juvenile							2	6					

male was twice observed driving off a juvenile, at the same time giving loud, aggressive sucking notes and wing extension displays.

With the exception of these adult-juvenile encounters, which probably result in dispersal of the young, very little aggression occurred between June and January (table 3); activity was low and restricted to the "range," with the result that very little interpair contact was observed.

TIME OF BREEDING

A summary of literature references, unpublished field notes, and personal observations indicates that Nuttall Woodpeckers have active nests between 25 March and 14 June ($n = 46$), the average egg date being 28 April. Of the 46 records, 37 fall between 12 April and 6 May.

Timing of nesting varied at the Hastings Reservation, but incubation never was noted before the second week of April nor later than the first week in May. One nest studied extensively in 1941 by T. Riney showed the following sequence: excavation, 4-16 April (13 days); egg laying, 14-16 April (3 days); incubation, 17-30 April (14 days); feeding young, 1 May-29 May (29 days), with the first of three young fledging on 28 May and the last on 29 May.

Bent (1939) reports an incubation period of about 14 days for *Dendrocopos nuttallii* and about 13 days for *D. scalaris*, while Ligon (1970) observed *D. borealis* incubating for 10 days, with fledging taking place 26-29 days after hatching. Most woodpeckers apparently follow this pattern of incubating between 10 days and 2 weeks, and feeding nestlings for 3 or 4 weeks (e.g., Bent, op. cit.; Lawrence 1967).

PAIR RELATIONSHIPS

Male-female contact. Nuttall Woodpeckers apparently were permanently paired and occupied the same ranges year-round. Permanent pairing has been recorded for many species of woodpeckers when they are resident, including *Dendrocopos villosus* (Lawrence 1967), *D. pubescens* (Kilham 1962; Lawrence,

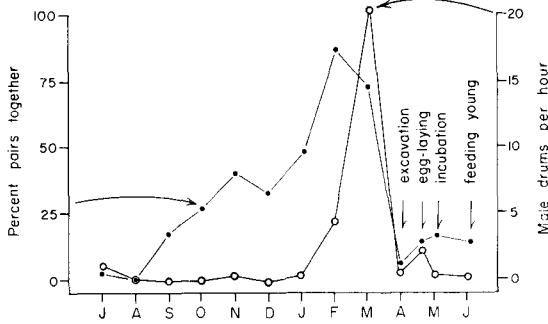


FIGURE 3. Annual cycle of the Nuttall Woodpecker at the Hastings Reservation (based upon 14,347 min of observation). The precise timing of breeding varied slightly from year to year (see text).

op. cit.), *D. albolarvatus* (Robinson 1957), *Asyndesmus lewis* (Bock 1970), and *Dryocopus pileatus* (Kilham 1959). In all of these species there is at least some contact outside the breeding season, and often preliminary courtship may begin as early as mid-winter.

Although pairs of Nuttall Woodpeckers appeared to reside together permanently, they often roosted in widely separated cavities at the reservation, and there was a marked annual fluctuation in the amount of actual contact (fig. 3). Following fledging during July and August, adults became very inactive and inconspicuous, and they were almost always solitary once adult-juvenile contact terminated. Then gradually through the fall and winter months males and females, which seemed by their locations to be pairs of the previous nesting season, spent increasing amounts of time foraging together, with courtship and pair-bond reinforcement reaching a peak in February and March (fig. 3). This was followed by periods of marked separation during which the males excavated nest sites. Pair contact increased somewhat for the remainder of the breeding season, when birds were copulating, incubating, and caring for the nestlings.

Unfortunately, we have no data on pairing in first-year birds although it very likely occurs in February and March when established pairs are most involved in courtship.

Communication and courtship behavior. During the fall and winter, pairs of Nuttall Woodpeckers often were "in touch" vocally, exchanging *check* and multiple *check* calls while foraging. These are probably equivalent to the "location calls" described by Lawrence (1967) for *Dendrocopos villosus* and *D. pubescens*.

When paired male and female Nuttall Woodpeckers came into close contact, both in

the nonbreeding season and also at the nest, they gave soft sucking or wheezing calls which were similar but less intense than the loud sucking notes which occurred during territorial encounters (see above). Lawrence (op. cit.) similarly recorded "mutual recognition or contact notes" which occurred when members of mated pairs met during the breeding season and which appear to be soft versions of her "aggressive-social notes." She and Kilham (1962) have considered these contact notes as a form of greeting, expressing a close pair-bond relationship and mutual tolerance. However, the similarity of these calls to the loud, aggressive calls suggests that they may in fact be an expression of hostility between sexes.

Davis et al. (1963) noted that the *chrrp*-call of the Western Flycatcher (*Empidonax difficilis*) occurred both during aggressive encounters and also when pairs met at their nests. Similarly, the Lewis Woodpecker gives a "chatter-call" when defending winter mast stores or nest sites against intruders, and also during courtship (Bock 1970). Hinde (1966) discusses the basic ambivalence of pair relationships in birds, noting the conflict between courtship and threat. "Contact notes" such as those occurring in *Dendrocopos nuttallii* and other woodpeckers may have evolved as a means for release of potentially dangerous intrapair hostility.

In late January or February, pair relationships among Nuttall Woodpeckers at the Hastings Reservation changed markedly. Both sexes, but especially the males (fig. 3), began to drum on their ranges. Pairs, but particularly females, also gave a *yipe* note which usually was in response to drumming. This reached a peak during March, but also was common during egg-laying following nest excavation (fig. 3). Although the pair-bond obviously was reinforced prior to nest excavation, copulation did not begin until after construction was nearly completed. We observed that females usually gave *yipe* notes prior to coition, perhaps as an invitation to the males. The following is a description of copulation between the male and female of pair 2 (fig. 2) observed on 10 May 1955. The female flew to a valley oak near the nest site and gave a *yipe* note. As the male appeared, the female assumed a horizontal position across a limb about 1.5 inches in diameter; the male flew in silently and mounted the female. While copulating, the female swung her tail sharply to the right and the male kept his left wing extended, swinging over to the left side of the female during the 20 sec of contact.

TABLE 4. Attentiveness of male and female Nuttall Woodpeckers during nest excavation (based upon 1222 min observation).

	Attentive periods (min)				Inattentive periods			
	n	\bar{x}	range	%	n	\bar{x}	range	%
Males	19	27.2	2-66	42.2	19	37.2	6-152	57.8
Females	5	10.8	4-21	4.4	8	146.0	3-365	95.6

NESTING BEHAVIOR

Excavation. Nuttall Woodpeckers excavated new nests each year; winter roosts were not used, nor were old nest cavities. It is not clear from our data which sex selects the site, but approximately 20 hr of observation indicate that males construct nests with very little assistance from the females. Not only did females rarely visit three nest sites observed during construction (table 4), but when they did, it was not to assist in excavation. Males were seen to drop wood chips from cavities 82 times, the females, never. In addition, the males began to roost in the cavities when they were near completion.

Egg-laying and clutch size. Miller and Riney both observed nests during this period. In both cases, copulation and egg-laying began in the last few days of nest construction. The females began to spend more time at the nests (table 5), usually copulating two or three times on successive mornings during laying. In addition, the females became more involved in completion of the nest. In 1385 min of observation the males dropped chips 44 times, the females, 20.

A survey of literature references and unpublished data indicates that clutch size varies as follows ($n = 42$): 3 eggs, 2 records; 4 eggs, 19 records; 5 eggs, 16 records; 6 eggs, 5 records.

Incubation. The trend of increasing interest in nest activities on the part of the female continues during incubation. Riney made an extensive study of incubation behavior at a nest on the reservation in 1941. As during construction, the male continued to play a predominant role, incubating the eggs at night and a majority of the day (table 6). However, atten-

TABLE 5. Attentiveness of male and female Nuttall Woodpeckers during egg-laying (based upon 1385 min observation).

	Attentive periods (min)				Inattentive periods			
	n	\bar{x}	range	%	n	\bar{x}	range	%
Males	28	22.9	1-92	46.3	27	27.5	1-79	53.7
Females	21	11.6	1-27	17.6	23	49.6	2-159	82.4

TABLE 6. Attentiveness of male and female Nuttall Woodpeckers during incubation (based upon 4156 min nest observation).

	Attentive periods (min)				Inattentive periods			
	n	\bar{x}	range	%	n	\bar{x}	range	%
Males	50	48.5	1-115	59	47	35.8	1-79	41
Females	34	45.2	5-79	37	36	72.6	5-189	63

tiveness of both sexes, and particularly the female, increased sharply between the last day of laying and the first days of incubation (tables 5 and 6). During the incubation period, at least one adult was attentive at the nest for 95% of 4156 min nest observation. Actual incubation occurred for 85%, the adults perching outside the cavity for the remainder of their attentiveness.

The nestling period. Nuttall Woodpeckers fed their young an average of 7.2 times per hr, based upon over 208 hr of observation of six different nests on the Hastings Reservation. Females for the first time played an approximately equivalent role, feeding 3.8 times per hr as compared with 3.4 for males.

Both sexes increased feeding rates during the fledging period. Overall rates increased from an average of 4.8 per hr during the first week of nestling life, to 6.3 during mid-fledging, to 9.4 during the fourth and last week. Hourly feeding rates generally were higher in the morning than in the afternoon (table 7).

Males brooded the young at night through about the first 10 days of nestling life, after which both parents roosted away from the nest. Males did 50.2% of the diurnal brooding

TABLE 7. Hourly variation in feeding rates of Nuttall Woodpeckers.

Hour	n	Total feedings	Average/hr	Rank
5-6	14	161	11.50	1
6-7	21	209	9.95	2
7-8	16	114	7.13	5
8-9	22	176	8.00	3
9-10	23	159	6.91	6
10-11	22	162	7.36	4
11-12	21	136	6.48	11
12-13	12	80	6.67	8
13-14	18	97	5.39	13
14-15	18	115	6.39	12
15-16	16	105	6.56	9
16-17	11	74	6.73	7
17-18	9	43	4.78	14
18-19	4	26	6.50	10

and the females, 49.8%. Young were brooded 70.4% of the daylight hours during the first week, but this declined rapidly and occurred not at all the last 2 weeks before fledging.

Males were observed removing feces from nests on 63 occasions while the females did so on 24 visits to the nests. Nest sanitation does not seem to be a major occupation of Nuttall Woodpeckers, as this represents only one fecal mass removed per 144 min of nest observation.

Fledging. Riney observed two young Nuttall Woodpeckers leaving the nest which he studied. At 05:51 on 28 May, the adult male flew to the nest and fed the young. Two minutes later a juvenile, which had continued to beg vigorously with its head at the cavity entrance, left the nest tree and flew unsteadily to a living tree 25 yards away. This bird was heard calling all day and occasionally one of the adults would feed it. The next morning at 06:13 the male came in and gave part of its food to another nestling, and then hunched down the tree about 8 inches. This juvenile fell out of the cavity apparently in an attempt to reach the food in the male's bill. The male immediately flew off, as the young bird landed on a limb 10 ft below the nest. Soon thereafter the juvenile flew off in the direction of the adult bird.

Juveniles remain with adults for some time after fledging, following them about and begging for food. The adults apparently remain tolerant of these young through June and early July, but become aggressive and drive them off in late July and August (table 3).

Discussion. The Nuttall Woodpecker appears similar to most picids insofar as the males perform most of the nest excavation, diurnal incubation, and nest sanitation, in addition to incubating and brooding at night (see Kendeigh 1952; Lawrence 1967). Feeding young and diurnal brooding usually are activities shared more nearly equally by the sexes, and this appears to be true of *Dendrocopos nuttallii*.

The overall average feeding rate (7.2/hr) is within the range of other species in the family (Kendeigh, op. cit.). There is some controversy over the significance of hourly variation in feeding rates. Kendeigh noted that birds are most active in the early morning and evening, with the result that the adults may feed young more frequently at these times. Stickel (1965), for example, found this to be true for the Red-bellied Woodpecker (*Centurus carolinus*). However, Lawrence (1967: 116) noted that such a bimodal pattern is sub-

ject to marked daily variation "caused by the impact of impromptu events connected with the relationship between the parents, their pre-occupation and relative industry, or the defense of territory." In a species such as the Nuttall Woodpecker, which feeds to a considerable degree by gleaning surface insects, fluctuations in food availability related to such things as weather and insect emergences very likely also have an effect upon feeding rates. While birds we observed generally fed more in the morning hours than during mid-day, there was no corresponding evening peak (table 7). In addition, table 7 represents only the overall picture, which masks daily and hourly variations similar to those described by Lawrence.

INTERSPECIFIC COMPETITION AND AGGRESSION

Nuttall Woodpeckers interacted with a variety of other species at the Hastings Reservation. This included not only other woodpeckers but also, during the breeding season, a number of hole-nesting passerine species (table 8). The frequency of encounters during the breeding season was far greater than at other times of the year, suggesting that competition for nest sites is high. All of the interactions with passerine species observed during the nesting period took place at nests, often where the other birds were nesting or attempting to nest in old woodpecker holes in the same trees. A good example is the aggressive relationship which developed between a pair of Nuttall Woodpeckers and a pair of Ash-throated Flycatchers (*Myiarchus cinerascens*) which nested in the same partially dead sycamore. The flycatchers had taken over an old nest hole in the tree and were reacting very aggressively toward the woodpeckers. This persisted throughout the nesting cycle, the flycatchers being dominant and pugnacious toward the woodpeckers. On 25 occasions between 29 April and 28 May, one of the flycatchers chased a Nuttall Woodpecker flying to or from the nest tree. In five of these instances, the flycatcher actually attacked and grappled with the woodpecker in flight.

Similar aggressive situations were observed between Nuttall Woodpeckers and Plain Titmice (*Parus inornatus*) and House Wrens (*Troglodytes aedon*) sharing nesting trees, except that here the woodpeckers were dominant in nearly every encounter recorded.

Interactions with other woodpeckers seemed to be related to competition for food. MacRoberts (1970) found that Acorn Woodpeckers

TABLE 8. Aggressive interactions between Nuttall Woodpeckers and other species at the Hastings Reservation.

Species	Number of interactions			
	Jan.- Mar.	Apr.- Jun.	Jul.- Sept.	Oct.- Dec.
Acorn Woodpecker (<i>Melanerpes formicivorus</i>)	4	-	1	-
Downy Woodpecker (<i>Dendrocopos pubescens</i>)	1	6	4	-
Hairy Woodpecker (<i>Dendrocopos villosus</i>)	-	5	1	-
Sapsucker (<i>Sphyrapicus varius</i>)	-	-	-	6
Ash-throated Flycatcher (<i>Myiarchus cinerascens</i>)	-	32	4	-
Violet-green Swallow (<i>Tachycineta thalassina</i>)	-	5	-	-
Scrub Jay (<i>Aphelocoma coerulescens</i>)	2	-	1	2
Plain Titmouse (<i>Parus inornatus</i>)	-	15	-	1
House Wren (<i>Troglodytes aedon</i>)	-	19	-	-
Western Bluebird (<i>Sialia mexicana</i>)	-	4	-	-
Misc.	1	6	2	2
Totals	8	92	13	11

at the Hastings Reservation maintain and defend "sap trees," and observed 71 interactions between them and intruding Nuttall Woodpeckers. We have observed six interactions between *Dendrocopos nuttallii* and true sapsuckers (*Sphyrapicus varius*) which took place at the sap trees of the latter (table 8). Nuttall Woodpeckers apparently only rarely feed upon acorns (see "Feeding Ecology"), but we have observed them being chased from Acorn Woodpecker storage trees on several occasions. They may simply have strayed there by chance.

Interactions with the ecologically similar Downy Woodpecker took place both at foraging and nesting sites. On two occasions, a male Nuttall Woodpecker drove an intruding Downy Woodpecker from its nest tree. On four other occasions, the two species met while both were foraging, each being dominant twice. Once a female Nuttall gave a loud aggressive sucking note as it displaced a Downy foraging in a toyon (*Photinia arbutifolia*) bush.

We once observed a Hairy Woodpecker supplanting a Nuttall Woodpecker in a valley oak. Hairy Woodpeckers were recorded visiting Nuttall Woodpecker nest trees on four occasions. The latter never reacted overtly toward the larger species, but did maintain alert and

aggressive postures (bill-pointing) until the intruders flew off.

Our observations of intense interspecific aggression related to nest sites are in decided contrast to those of Lawrence (1967:103) who found "the woodpeckers' attitude toward other than their own species at this point in the nesting cycle [incubation and feeding] is remarkably lenient." This difference may be due to a greater abundance of potential nest sites in Lawrence's study area in a central Ontario mixed forest, as compared with the more xeric woodlands of the Hastings Reservation.

SUMMARY

Nuttall Woodpeckers (*Dendrocopos nuttallii*) were studied at the Hastings Reservation, Monterey County, California. Foraging occurred primarily in oaks, but pairs showed a preference for softer-wooded sycamores and willows as nest sites.

The birds employed a variety of foraging techniques, including trunk and limb gleaning and probing, foliage and twig scanning, flycatching, and sapsucking, as well as actual "classical" woodpecker excavation. Most foraging appears to be for surface and subsurface insects, although various fruits and berries, as well as sap, are taken in certain seasons.

Permanent pairs occupied and defended year-round ranges which were approximately 0.5 miles in diameter and which centered along drainage patterns. There was little intra-pair contact in the summer following nesting, but during the fall and winter males and females spent increasing amounts of time together, with courtship and pair-bond reinforcement reaching a peak in February and March.

Nesting occurred from mid-April to mid-June. Incubation lasted about 14 days, fledging, 29 days. Males excavated the nests and incubated and brooded the young at night, as well as performing most of the diurnal incubation and nest sanitation. The sexes shared diurnal brooding and feeding activities. Adults fed the young an average of 7.2 times per hr. This feeding rate tended to be highest in the morning hours and also increased generally during the nestling period. Adults were accompanied by fledged juveniles until mid-July, at which time they became intolerant of the young and drove them off.

Many aggressive interactions occurred during the nesting season between Nuttall Woodpeckers and several hole-nesting passerine species as well as other woodpeckers, suggesting a high level of competition for nest sites.

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Accepted for publication 3 February 1971.