NOTES ON THE FOOD HABITS AND FOOD DEFENSE OF THE ACORN WOODPECKER

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The Acorn Woodpecker (*Melanerpes formicivorus*), the most social of North American woodpeckers, is a common resident of mixed oak woodlands from Oregon south through California, east through Arizona, New Mexico and Texas, and south to Panamá. These woodpeckers live in year-round groups. Each group consists of 2–10 birds of both sexes and apparently all ages (Ritter 1938). In most groups males are reported to outnumber females, but this apparent discrepancy in sex ratio may be explained by the fact that juveniles possess the adult male plumage during at least part of their first year (Ritter 1938). Territory and food defense, nest hole construction, and the care and feeding of nestlings appear to be accomplished jointly by all members of the group. Aside from these rather sketchy points, little else is known about the social organization of these woodpeckers.

In its food habits, the Acorn Woodpecker is one of the most atypical of all woodpeckers. During the fall and winter the birds feed extensively on acorns and other mast which they store in prepared holes in the surfaces of oaks and pines. This aspect of their ecology has been repeatedly described (see literature cited in Ritter 1938 and in Bent 1939), but because of a predominance of interest in this unusual habit, other aspects of the woodpeckers' food habits have been largely neglected by most naturalists. This is unfortunate since it has led to the assumption that the food habits of these birds are far less diversified than is actually the case. In addition to storing and consuming dried acorns, the woodpeckers feed extensively on mature and immature green acorns before storage begins during the fall, and are proficient flycatchers and sapsuckers.

The purpose of this paper is threefold: 1) it describes some previously unreported or incompletely described aspects of the food habits of the Acorn Woodpecker; 2) it describes the defense of these foods from conspecifics and heterospecifics; and 3) it compares some aspects of the food habits of the Lewis' (*Asyndesmus lewis*), Acorn, and Red-headed (*Melanerpes erythrocephalus*) Woodpeckers. Since the food habits of the Acorn Woodpecker have been the subject of several previous papers (see literature cited by Beal 1911, Ritter 1938, and Bent 1939), a repetition of these earlier works is avoided.

STUDY AREAS

The study entailed 40 hr of observation between 20 October and 15 December 1966 of two Acorn Woodpecker groups 2.5 mi. NW of Orinda, California, near the southern end of San Pablo Reservoir, and about 500 hr of observation from 11 April to 15 September 1968 of 11 groups at the Frances Simes Hastings Natural History Reservation, Monterey County, California. The groups studied at Orinda lived in mixed oak-pine woodland, while those studied at Hastings lived in foothill and canyon-bottom mixed oak woodland.

FOODS OF THE ACORN WOODPECKER

STORED ACORNS

The present study adds little to previous descriptions of acorn storage, except to devaluate the relative importance placed by other investigators on it as a food source for the Acorn Woodpecker.

About half of the 11 groups studied at Hastings had exhausted their stored acorns before observations began there in April. This was due largely to acorn failure in all but the black oak (*Quercus kelloggii*) the previous year. Nevertheless, each group, irrespective of the state of its acorn supply, maintained its own territory and subsisted on other foods throughout the summer. Those groups which had acorn stores did not use these to any large extent but, like those groups without stores, subsisted on other foods.

It is apparent therefore that during the summer the woodpeckers can subsist on and prefer foods other than stored dried acorns,

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and that, even if stores remain from the previous winter, these may not be extensively used.

IMMATURE AND MATURE GREEN ACORNS

Ritter (1938:29, 84) mentioned that the Acorn Woodpecker uses immature acorns as food, but the present study suggests that their importance in the birds' diet is greater than has previously been supposed. In the groups observed at Hastings, immature acorns were eaten (especially those of the live oak, *Quercus agrifolia*, the black oak, *Q. kelloggii*, the valley oak, *Q. lobata*, and the blue oak, *Q. douglasii*) beginning in late July and continuing through early September, without any storing being involved. The immature nuts were picked, carried to "anvils," split open, and the meat immediately consumed.

In the second week in September, the woodpeckers at Hastings began storing mature green acorns. During this time they continued to feed extensively on acorns, but instead of immediately eating all they picked, they stored some. These immature acorns (and later, mature green acorns) were the major food source of all the groups studied at Hastings throughout August and early September, regardless of whether or not a particular group's acorn stores from the previous year had been exhausted.

SAPSUCKING

A third major food source is sap. The six most studied Hastings groups had one or two sap trees which they defended from other birds. (It is not known whether the other five groups maintained sap trees.) In each case, these were live oaks (*Q. agrifolia*) located within 100 m of the group's main storage tree. Live oaks were never used for acorn storage.

The woodpeckers drilled small holes 5–15 mm in diameter and 3–19 mm deep on the upper surfaces of middle and upper canopy branches of live oaks. The branches in one tree into which sap holes were drilled were 2.5–15 cm in diameter. The diameter and depth of the sap holes are related to the diameter of the limb in which they are excavated. Large limbs support wider and deeper holes than do small limbs. This is due to the depth of the bark since the sap holes always penetrate through the bark but not into the wood. In one particular live oak, about 1800 sap holes were counted, although only a part of the tree was used by the birds for this purpose.

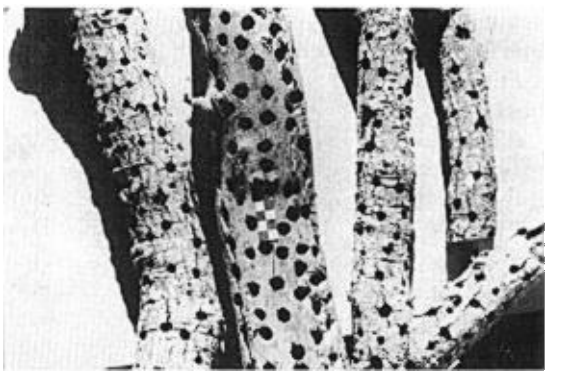

FIGURE 1. Acorn storage branch (center, with centimeter scale) and sapsucking branches (right and left). Note differences in diameter of acorn storage and sap holes. The sapsucking branches used for this photograph were dead and desiccated and consequently nonfunctional at the time they were removed from the tree.

The sap holes were more or less uniformly spaced. The distance between holes was apparently independent of branch diameter, with a mean nearest-neighbor measurement (mm) of 24.7 (SD = 5.2, $N = 131$) and 21.6 (SD = 5.4, $N = 107$) in two independent samples. This is approximately the same distance as between acorn storage holes drilled in dead smooth surfaced trees (e.g., sycamores or valley oaks). The mean nearest-neighbor measurement (mm) between storage holes was 24.2 (SD = 4.3, $N = 73$) and 20.5 (SD = 3.6, $N = 110$) in two independent samples. The mean of the entire set was 22.7 (SD = 5.0, $N = 421$). Variance analysis of the four samples shows that neither sap nor storage holes can be distinguished by separation distance ($F = 2.8$, $P < 0.05$). This suggests that a unitary behavioral mechanism may be involved in deciding the spacing pattern of storage holes as well as sap holes. Figure 1 shows a sapsucking and an acorn storage area for comparison.

Since there are two possible ways that sap and storage holes can be excavated to produce a uniform spacing pattern, I shall briefly describe the process used by the woodpeckers. On a certain section of limb, a bird will begin excavating a hole. After this hole is begun, but before it is finished, this bird or another one will begin excavating a second hole at the "correct" distance from the first. Other holes are excavated in a similar manner, each adjacent to, but at the "correct" distance from, its nearest neighbor. Since hole construction is a relatively slow process, many birds will have participated in the excavation of a particular hole before its completion. Con-

sequently, since the birds are continually making new sap and storage holes, there are numerous holes in various states of preparedness.

The woodpeckers repeatedly visited and probed into these sap-filled holes. I would estimate that during the height of the sapsucking period (June and July) each hole was visited, on an average, 4–10 times per hr, but since different holes were differentially used, it is difficult to make a more precise estimate. In the process of excavating these sap holes the woodpeckers may eat some of the excavated bark, but whether or not this in fact occurs is not known.

Whether or not sap is a year-round food source for these birds is unknown. Further research on an annual basis will be necessary to establish its seasonality. I did not become aware of sapsucking until the early part of June, but from the number of sap-producing holes in the sap trees at that time, this food source had been of major importance for a long time before I became aware of it.

Fisher and Peterson (1964:35) mention that the Acorn Woodpecker sucks sap from sapsucker holes, but in my study area they drilled their own sap holes and used these exclusively. Since the red-headed race of *Sphyrapicus varius* is migratory in the Hastings area, none was observed during the present study, and consequently it is not known whether the Acorn Woodpecker robs sap from these birds during the winter months when sapsuckers are present.

As immature acorns became an important food source in August and September, the birds ceased frequenting their sap trees. By the end of the study the woodpeckers seldom entered sap trees and ceased protecting them from other birds. This indicates that sapsucking is a seasonal activity, but just when it begins is in doubt.

FLYCATCHING

The behavioral aspects of flycatching by the Acorn Woodpecker have been adequately described by Bent (1939) and by Ritter (1938). The behavior is almost identical to the flycatching behavior of the Lewis' Woodpecker described by Bock (1968, in press) and to that of the Red-headed Woodpecker (Bent 1939) except that the Acorn and Red-headed Woodpeckers seldom execute what Bock (1968:81) has called "non-specific flights" (i.e., remaining in the air for several minutes while taking several insects before landing). Instead, Acorn and Red-headed Woodpeckers engage almost exclusively in "specific flights" or catch only one insect per flight. In addition, the Acorn Woodpecker never forages for insects directly on the ground or in low brush as is common in the Lewis' Woodpecker.

I feel, however, that previous researchers have underestimated the importance of flycatching as a foraging method of the Acorn Woodpecker. At Hastings flycatching was a common activity throughout the study, especially during the nestling period when the newly hatched birds were fed on insects caught in this manner. Although I did not attempt to quantify the time spent flycatching or the amount of food obtained by it, flycatching was undoubtedly the major foraging method of these birds throughout April and May, only to be replaced in importance by sapsucking in June and July.

During the nestling period, the woodpeckers temporarily store insects. After each sortie, the bird would return to its hawking perch and pound the captured insect into a crevice. This was repeated several times before it carried all of the insects to the nestlings. Bock (1968:97) has reported that the Lewis' Woodpecker likewise stores insects. The explanation he proposes is that "such behavior would increase the ability of Lewis' woodpeckers to capitalize upon a temporarily superabundant food source by shortening the time between each capture" when feeding the young. This explanation certainly seems plausible for the Acorn Woodpecker as well.

OTHER FOOD SOURCES

According to Ritter (1938:31) the Acorn Woodpecker has all but abandoned "the traditional woodpecker way of getting nourishment from the insect world. . ." (i.e., by boring and gleaning for insects and insect larvae). I am in complete agreement with Ritter on this point as I never definitely observed birds gleaning and never observed an Acorn Woodpecker drilling for any length of time at anything other than sap holes, acorn storage holes, nest holes, and at various objects such as acorns which were split open before being eaten. In addition, Beal's (1911) analysis of stomach contents indicates that wood-boring insects and larvae are almost entirely absent from the birds' diet.

Ritter (1938:28) stated that "on some occasions I have seen the birds picking at something in the oaks, when the spring buds are well advanced, in such a way that they appeared to be feeding on the buds, but of this

TABLE 1. Rate of supplanting of heterospecifics by Acorn Woodpeckers in Group A's storage trees at Orinda, California, during 16.5 hr of observation.

Species	Interactions		No. passes to supplant intruder		No. woodpeckers involved		Interactions accompanied by "karrit-cut"
	No.	Rate/hr	mean	range	mean	range	
Fox squirrel (*Sciurus niger*)	123	7.5	7.3	1–73	3.2	1–5	113
White-breasted Nuthatch (*Sitta carolinensis*)	39	2.4	1.1	1–3	1.0		1
Steller's Jay (*Cyanocitta stelleri*)	36	2.2	1.7	1–5	1.3	1–4	
Plain Titmouse (*Parus inornatus*)	9	.5	1.3	1–4	1.0		
Red-shafted Flicker (*Colaptes cafer*)	9	.5	1.1	1–2	1.1	1–2	
Scrub Jay (*Aphelocoma coerulescens*)	3	.2	1.0		1.0		
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	2	.1	1.0		1.0		
Nuttall's Woodpecker (*Dendrocopos nuttallii*)	1	.06	1.0		1.0		
Starling (*Sturnus vulgaris*)	1	.06	1.0		1.0		1
Ruby-crowned Kinglet (*Regulus calendula*)	1	.06	1.0		1.0		
Unidentified small birds	21	1.3	1.2	1–2	1.05	1–2	
Total	245	14.88					115

I have never been quite certain." I observed the same type of behavior at Hastings during the latter part of April and early May, but, like Ritter, I was never able to discern just what it was that the woodpeckers were getting from among the oak blossoms.

According to Ritter (1938) and Beal (1911) other items eaten by the Acorn Woodpecker include various fruits and the eggs of other birds. Although I never saw a woodpecker eat any of these items, I did see one eat a lizard (probably *Sceloporus occidentalis*). Whether the lizard was alive or dead when it came into the woodpecker's possession is unknown. The bird carried it to an "anvil," pounded on it, and consumed at least part of it.

DEFENSE OF FOOD SUPPLY

The members of each group supplant heterospecifics from their acorn storage and sap-sucking trees, the acorn-bearing oaks from which they gather acorns, their roosts and nest holes, and occasionally from anvils and hawking perches. In addition, the members of each group supplant any conspecific of a different group that enters their territory. The area of defense in this latter case is much larger and less localized than that defended from heterospecifics.

HETEROSPECIFIC DEFENSE

Most of the discussion which follows is based on observations made of the Orinda A group in the fall of 1966.

Acorn Woodpeckers supplant heterospecific birds and small mammals that enter their storage trees. Supplanting usually consists of one or more woodpeckers making one or more aerial passes at the intruding animal until the intruder leaves, at which time it may or may not be pursued. In this type of interspecific interaction, physical contact is seldom made between the woodpecker and the intruder. Supplanting may be accompanied by a vocalization ("karrit-cut") which apparently functions to alert and attract the attention of other group members to the intruder's presence.

Table 1 summarizes data on supplantings by members of Group A (5 birds) of heterospecifics that entered their storage trees during 16.5 hr of observation on six days in November and December 1966. At Orinda, all hetero-

specifics which entered the storage trees were supplanted (one exception; see below). Consequently table 1 not only gives the frequency of supplantings but also indicates the frequency with which heterospecifics entered the storage trees.

The woodpeckers were always successful in quickly supplanting trespassing birds. This usually required a minimum of effort, a single woodpecker making a single aerial pass at the intruder. Fox squirrels (*Sciurus niger*, an introduced species), on the other hand, were often persistent in their efforts to steal nuts and would remain under continual attack while frantically attempting to extract an acorn. On one occasion five woodpeckers made 73 aerial passes at a squirrel before it was able to extract an acorn and leave the storage tree.

No bird was definitely seen taking any of Group A's acorns and it is probable that some of the species supplanted never used acorns as food. Only fox squirrels and Steller's Jays (*Cyanocitta stelleri*) were seen with acorns, but in those cases involving the jays it is not certain that these came from the woodpeckers' stores.

Between 30 November and 4 December, the squirrels "took" one of Group A's four storage trees. I did not see how this was accomplished, but between these dates the woodpeckers ceased attempting to supplant heterospecifics that entered this tree. On 4 December, during one observation period, there were four squirrels feeding on the few acorns remaining in this tree. During each successive visit between 4 and 10 December the woodpeckers continued to lose ground. The last time I saw Group A they were still defending one storage tree, having lost the others. On my visit of 15 December, all individuals of Group A were gone and their acorn stores had been completely exhausted by the squirrels.

Two sets of comparative observations were conducted at Hastings on the frequency of heterospecific supplanting associated with intrusion into acorn storage trees. The first set of observations (26 hr) was conducted between 30 August and 5 September on a group of six birds which had exhausted its acorn supplies. During the observation period nine heterospecifics entered the group's storage tree and five were supplanted. The following birds entered the storage tree but left of their own accord within a few seconds: Western Tanager (*Piranga ludoviciana*), Western Bluebird (*Sialia mexicana*), Oregon Junco (*Junco oreganus*), and Ruby-crowned Kinglet (*Regulus calendula*). The following entered the storage tree and were supplanted: Nuttall's Woodpecker (*Dendrocopos nuttallii*), Hairy Woodpecker (*Dendrocopos villosus*), Plain Titmouse (*Parus inornatus*), and White-breasted Nuthatch (*Sitta carolinensis*) (twice).

The second set of observations (24.5 hr), conducted also between 30 August and 5 September, were of a group which had not exhausted its acorn supplies. Two heterospecifics entered this group's storage tree: a Sparrow Hawk (*Falco sparverius*), and a Red-tailed Hawk (*Buteo jamaicensis*). The woodpeckers attempted to supplant the Sparrow Hawk by making aerial passes at it; in addition, the hawk repeatedly flew at the woodpeckers. The woodpeckers simply fled from the Red-tailed Hawk.

During the Hastings study, only one tree squirrel (*Sciurus griseus*) was seen in any tree used by the woodpeckers. In this case, four woodpeckers (all of the members of the group) made repeated passes at the squirrel and ultimately supplanted it from the acorn-bearing oak. This tree was also a hawking and anvil site.

Based on these data and on my unquantified observations, the frequency of heterospecific supplantings at Hastings associated with heterospecific intrusion into storage trees was very much less than that observed at Orinda. This can probably be attributed to three major factors. The first and most obvious reason for the difference is that the rate at which heterospecifics entered the woodpeckers' storage trees was far lower at Hastings than at Orinda. Orinda Group A maintained four large storage trees and no group at Hastings maintained anything approximating this extent of storage area. Consequently, by chance one would expect more heterospecific intruders at Orinda than at Hastings. Second, some heterospecifics at Orinda made major efforts to rob the woodpeckers' stores. This was especially true of tree squirrels which were far more common at Orinda than at Hastings. For example, at least five squirrels were always seen in the immediate vicinity of Group A's storage trees while at Hastings only one tree squirrel was ever seen in the vicinity of any group's storage trees. What relationship, if any, exists between the fact that at Orinda the squirrels were an introduced species and the rate of competition between the woodpeckers and squirrels is unknown. A final reason may be found in the fact that all of Orinda Group A's storage trees could

TABLE 2. Rates of aggressive interaction between Acorn Woodpeckers and heterospecifics in sap trees during 24.5 hr of observation in two Hastings Reservation colonies.

Species	Interactions		No. passes to supplant intruder		Mean no. woodpeckers involved	Interactions accompanied by "karrit-cut"
	No.	Rate/hr	mean	range		
Nuttall's Woodpecker (*Dendrocopos nuttallii*)	71	2.9	1.1	1–2	1.01	9
Anna's Hummingbird (*Calypte anna*)	31	1.3	1.0		1.0	1
Plain Titmouse (*Parus inornatus*)	7	.3	1.0		1.0	0
Mourning Dove (*Zenaidura macroura*)	1	.04	1.0		1.0	0
Brown Towhee (*Pipilo fuscus*)	2	.08	1.0		1.0	0
House Finch (*Carpodacus mexicanus*)	1	.04	1.0		1.0	0
Wrentit (*Chamaea fasciata*)	2	.08	1.0		1.0	0
Unidentified small birds	7	.3	1.0		1.0	1
Total	122	5.04				11

be entered via arboreal pathways from closely adjacent trees. At Hastings, on the other hand, most of the storage trees could not be entered except by crossing open areas on the ground. Consequently, access to Group A's storage trees was an easy matter for arboreal mammals.

Unharvested acorn supply. In addition to the apparent year-round defense of acorn storage trees, the woodpeckers during the late summer and fall defend the acorn bearing oaks from which they harvest acorns (Ritter 1938: 98ff). At Hastings, several species, especially the Scrub Jay (*Aphelocoma coerulescens*) and Steller's Jay, were supplanted from these oaks. However, since the woodpeckers used a large number of oaks simultaneously and since it was impossible to watch all of them, I was not able to collect many data on this aspect of food defense. I would estimate that, in an "average" group at Hastings, one jay entered and was chased from these acorn bearing oaks every 2 or 3 hr of observation. This apparently low rate of interspecific interaction was undoubtedly due to the abundance of acorns and the uncommonness of heterospecific competitors for these food sources in the study area. Ritter (1938:101) recorded an instance in which interaction between jays and woodpeckers over unharvested acorns was apparently very severe.

The woodpeckers usually had little or no difficulty in quickly supplanting jays and other heterospecifics from acorn-bearing valley and black oaks but often had great difficulty in supplanting these intruders from live oaks since the woodpeckers are relatively inept at moving quickly among the small, densely knitted terminal branches of these trees. Jays, however, can easily maneuver in this type of foliage. Consequently, if the woodpeckers could not fly at the intruder, they would hop along the branches until close to the intruder who then generally flew out of or to another part of the tree.

Sap trees. A third area defended by the woodpeckers is their sap trees. Table 2 records the data for 24.5 hr of observation of two different sap trees on the Hastings Reservation 21–26 June. The rate of interaction between the woodpeckers and heterospecifics recorded in table 2 probably accurately reflects the rate with which heterospecifics entered the sap trees, since all heterospecifics which entered were chased out.

The woodpeckers often had difficulty in driving birds from the sap trees, for the same reasons that they had difficulty in driving jays from the acorn-bearing live oaks. All heterospecific birds who entered these sap trees were far more adept in maneuvering in the canopies of live oaks than were the woodpeckers. In many cases the woodpeckers could not get a clear aerial path to the intruder and had to hop and climb about among the branches in order to get close to the in-

truder. The woodpeckers apparently protect these sap trees only during the summer months, the period when they are feeding on sap.

Although I do not have comparative data from other localities, it seems that the rate of interspecific aggressive interaction between the Acorn Woodpeckers and other birds over sap "stores" was high. About five intruders per hour were chased from these trees.

Hawking perches, anvils, nests, and roost holes. Lastly, the woodpeckers supplant heterospecifics from their hawking perches and from the immediate vicinity of their anvils, roosts, and nest holes. Only those supplantings associated with anvils and hawking perches can be said to have any relation to food defense. In these cases, the presence of a heterospecific at a hawking site could interfere with flycatching, and birds near anvil sites might be attempting to retrieve acorn crumbs left from previous meals. Additionally, as the woodpeckers sometimes store insects near their hawking perches, defense of these areas might be associated with defense of these insect stores. When anvils and hawking perches are in trees which are protected for other reasons (i.e., storage trees), it is difficult to determine exactly what is being defended.

DEFENSE OF TERRITORY FROM CONSPECIFICS

In addition to defending their storage trees, sap trees, unharvested acorn bearing oaks, roosts, nest holes, anvils, and hawking perches from heterospecifics, the members of each group defend a territory from conspecifics. This area of defense, which includes all locations defended from heterospecifics, is much larger than that defended from heterospecifics and encompasses a minimum of 5 acres. A conspecific intruding on any part of this area was always pursued until driven out of the territory. Territorial defense has not been discussed in earlier literature on the Acorn Woodpecker.

At Hastings the intrusion of conspecifics into other groups' territories varied markedly between groups and at different times of day. In some groups no intruders were seen. In others intrusion was a daily occurrence. During 306 hr of observation of four groups, 159 cases of conspecific intrusion were recorded, of which at least 18 cases involved two or more intruders. Ninety-one per cent of all conspecific intrusion occurred before noon (57 per cent of the observations were made before noon). Most conspecific intrusion occurred between 3 and 5 hr after sunrise. In some cases the intruder(s) remained on the other group's territory for several hours until finally driven off. Conspecific intrusion, however, rarely led to contact or fighting because the intruders normally retreated soon after the territorial owners showed signs of attacking them.

Only one case was observed in which one group actually took over an area occupied by another group. In this case, one group of five birds defended one half of a storage tree and their own sap tree while another group consisting of six birds defended the other half of the same storage tree and their own sap tree. Members of each group frequently invaded the territory of the other and fighting between members of the two groups was frequent. In some instances, two or more grappling birds would fall from the top of the storage tree to the ground before becoming disentangled. After these two groups had been observed for about one week, one of them left and the other occupied the entire area. Very likely, before I began observing these groups, one of them had initially occupied the entire area and the other had managed to occupy and defend a part of that area for themselves. Ultimately, either the intruders or the residents were ousted.

DISCUSSION OF FOOD DEFENSE

Interspecific and intraspecific aggression is a common feature of the Acorn Woodpecker existence, and competition over food is undoubtedly the primary functional reason for this aggression. This type of competition is direct, with the competing individuals frequently coming into physical or near-physical contact. This makes "it possible not only to identify all competitors but also to quantify the relative comparative effects of the various species involved" (Bock 1968:126). It should be stressed, however, that all heterospecifics that are supplanted by the woodpeckers are not necessarily involved in any food competition with them. Apparently at Orinda and at Hastings all heterospecifics which entered the woodpeckers' storage trees and sap trees were supplanted with little or no discrimination made between intruders. Consequently, at least in some cases, the frequency with which a particular species was supplanted did not necessarily indicate the degree of competition between it and the woodpeckers, but only the frequency with which it, for whatever reasons, entered the woodpeckers' defended areas. For example, it is certain that Nuttall's

Woodpeckers, Anna's Hummingbirds (*Calypte anna*), and Plain Titmice enter the woodpeckers' sap trees for the purpose of getting sap; but Mourning Doves (*Zenaidura macroura*) and Brown Towhees (*Pipilo fuscus*), which were also chased from these same trees, showed no signs of attempting to take the woodpeckers' food. Likewise, at Orinda the fox squirrel was by far the major competitor, but, from a purely tabular point of view, all birds combined would appear to have been equally important as competitors. Nevertheless, as Bock (1968, in press) has indicated for Lewis' Woodpecker, those species most interested in robbing stores are the ones that come the most often, and likewise they are driven off more intensively by the woodpeckers. In the case of heterospecifics, however, it is clear that the woodpeckers' behavior is designed not only to protect food stores and sources but nesting and roosting sites as well.

The proximate factors stimulating conspecific intrusion into the territories of other groups are not known. In no case was a conspecific intruder seen taking food within the territory of another group. This, however, does not mean that the maintenance of group territories in these birds and the defense of this area from conspecifics of other groups is not related to the defense of food within the boundaries of the territory. The members of each group gather all, or certainly the major portion, of their food from within their own territory, and by ousting intruding conspecifics, they undoubtedly protect these food sources as well as their nesting and roosting sites from conspecifics.

INTERSPECIFIC COMPARISON OF HABITATS

The Lewis', Red-headed, and Acorn Woodpeckers have many similarities in food habits (Beal 1911; Bent 1939; Bock 1968, in press; Kilham 1958a, 1958b, 1963). All flycatch, store mast, and defend their stores, each in a slightly different way, from conspecifics and heterospecifics. Unlike the Acorn Woodpecker, however, neither the Lewis' nor the Red-headed Woodpecker lives in groups. Generally speaking, each individual stores and feeds on its own mast during the winter, maintaining a territory at this time. During the spring, both the Lewis' and Red-headed Woodpecker usually migrate to summer breeding grounds where they flycatch and feed on various fruits.

Bock (1968:11–12) has characterized the summer breeding habitat of Lewis' Woodpecker as follows: "one nearly universal characteristic of their breeding habitat is that of openness. Some trees are necessary for nesting and as hawking perches, but a dense coniferous forest or a woodland with closed canopy would restrict vision and aerial maneuvers and eliminate the brush and grass understory which supports important insect prey populations. . . ." This type of habitat appears to be very similar to that of the Red-headed Woodpecker (see Bent 1939).

The winter habitat of Lewis' and Red-headed Woodpeckers must have areas for storage and an adequate supply of mast. Consequently, they are found at this time of year in the immediate vicinity of oak woodlands, commercial nut orchards or other nut-producing trees (Bock 1968; Kilham 1958a). During the winter Lewis' Woodpeckers and Acorn Woodpeckers are often found in the same area and competition between them is extensive (Bock 1968). Neither of these species is sympatric with the Red-headed Woodpecker.

In favorable habitats both the Lewis' and Red-headed Woodpeckers will remain year round; the fact that the former are sometimes in pairs indicates that, when the habitat contains sufficient supply of both winter and summer food sources, these woodpeckers are resident (Bent 1939; Kilham 1963; Bock 1968).

The Acorn Woodpecker on the other hand uses many of the same foods, and in a very similar manner to Lewis' and Red-headed Woodpeckers, but is resident and lives in groups. Its habitat (usually mixed oak woodland) consists of one or more closely adjacent storage trees that are usually separated by open grasslands from other trees. In addition, other open areas, such as land cleared for pasture, are usually found in each group's territory. Within easy flying distance of the storage trees are acorn-bearing oaks which in most instances would normally include trees suitable for sapsucking. The Acorn Woodpecker habitat, then, contains one or more trees suitable for storage, acorn production, roosts, nesting holes, and, at least in some cases, for sapsucking, and an area (or areas) suitable for flycatching and hawking perches; thus, a heavy-canopied woodland or dense coniferous forest is not suitable. This single habitat combines elements of both the Lewis' and Red-headed Woodpecker's winter and summer habitats.

If these three species have similar food habits, the question naturally arises as to why

they are so different with respect to social and migratory behavior. It is impossible at present adequately to answer this question, since the comparative ecological and behavioral research is incomplete. Nevertheless, the sedentary nature of the Acorn Woodpecker is undoubtedly dependent on the presence of year-round food sources occurring in a nondispersed form. Although the Lewis' and Red-headed Woodpeckers are dependent on highly concentrated and locally abundant food sources, as is the case in the Acorn Woodpecker, their migratory behavior suggests that few habitats contain both mast and insects in sufficient quantities to permit year-round occupancy. Another important question arises at this point. The Acorn Woodpecker is highly social year round, whereas neither the Lewis' nor the Red-headed Woodpecker is. Bock (1968:141, 142) has suggested "that the communal behavior of *M. formicivorus* may have evolved specifically as a means of protecting acorn stores." This may in fact be the case, but unfortunately answers to questions concerning the adaptive features of Acorn Woodpecker sociality will have to await more detailed study of the social organization and genealogical relationships of group members.

SUMMARY

The results of this study indicate that the food habits of the Acorn Woodpecker are more complex than has previously been supposed. Instead of subsisting almost exclusively on stored, dried acorns, the birds eat immature and mature green acorns, flycatch, sapsuck, probably do very little boring or gleaning for insects and insect larvae, eat something associated with oak blossoms, and occasionally eat fruit, birds' eggs, and lizards. In addition, the members of each group defend their acorn storage and sap trees, the acorn bearing oaks from which they gather acorns, their roosts and nest holes, and occasionally their anvils and hawking perches from heterospecifics, and a larger area, the territory, from conspecifics.

The study further indicates considerable apparent similarity in food habits and habitat among the Acorn, Red-headed, and Lewis' Woodpeckers, but with obvious differences in social and migratory behavior.

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