SOCIAL ORGANIZATION AND BEHAVIOR OF THE ACORN WOODPECKER IN CENTRAL COASTAL CALIFORNIA

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INTRODUCTION

The Acorn Woodpecker (*Melanerpes formicivorus*) is nonmigratory and lives in year-round groups composed of both sexes and all ages. Its range includes the western and southwestern United States, Mexico, Central America, and northern Colombia (Ridgway 1914, A.O.U. 1957, Meyer de Schauensee 1964). In California, it extends from sea level to over 2000 m elevation at the limit of arboreal oak distribution and is found in oak woodland, coastal forest, and montane forest where oaks occur (Miller 1951). It is a species that stores food on a large scale. All group members help lay in the winter stores and all partake of the amassed provisions. Acorn Woodpeckers breed cooperatively. Group members jointly incubate the eggs and brood and feed the young. The members of each group jointly defend and share an all-purpose territory.

Recently such cooperative systems have received increased attention because they present apparent contradictions to natural selection (Wynne-Edwards 1962; Hamilton 1964, 1971, 1972; Lack 1968). This has led to a reevaluation of some aspects of natural selection theory and to modeling of the conditions under which cooperative behavior could evolve by natural selection.

The purpose of our research was threefold. First, we undertook to elucidate the breeding system and the genealogical relationships in Acorn Woodpecker groups. Second, as the species has received only cursory attention in the past (Ritter 1938, Bent 1939), we designed the research to gather information on a wide variety of topics that would aid in closing the numerous gaps in the knowledge of the species. Finally, the results provide information that may lead to a more critical analysis of the evolution of this particular social system.

The study was based mainly on field observations from blinds. Between 1971 and 1974, 149 birds were color banded. Each was given a distinctive set of color bands.

DESCRIPTION: COLORATION, MOLT, AND ANATOMY

The Acorn Woodpecker is a medium-sized picid, measuring about 24 cm in length. It is slightly dimorphic, males being larger than females. Ridgway (1914: 101) provides a description of the species. "General color black (glossed with blue or green on side of head and neck, back, scapulars, and chest), the rump, upper-tail coverts, and upper parts (posterior to chest) white; lower chest and upper breast (sometimes whole chest) streaked with black and white; forehead and foreneck (connected by a stripe across loral and malar regions) yellowish white to light yellow; a white patch at base of primaries; adult male with crown, occiput, and nape bright red, adult female with crown black."

This describes the species over most of its range. In the Colombian subspecies (*flavigula*) adult females have no red on the head while in adult males it is confined to the nape (Meyer de Schauensee 1964, Goodwin 1968). Details of molt and juvenile coloration, which are unusual in this species, are described elsewhere (Troetschler 1974, Spray and MacRoberts 1975).

Although the Acorn Woodpecker has diverged markedly from its relatives both in diet and in social living habits, it has not diverged anatomically. Structural features initially evolved in association with feeding habits related to clinging on vertical surfaces and excavating into wood for wood-boring insects have been put to use in other ways. The long flexible tongue, which evolved originally for probing into wood and under bark for insects and their larvae, is used primarily for probing into similar locations for bits of acorn. The tongue barbs typical of insectivorous woodpeckers have been modified into "brushes" ideally suited for taking up sap. The tongue of the Acorn Woodpecker is most similar, among North American woodpeckers, to the tongue of the Yellow-bellied Sapsucker (*Sphyrapicus varius*) (Lucas 1895).

The muscular and skeletal structure of the head and neck of woodpeckers correlates closely with the feeding habits of the species (Burt 1930, Spring 1965). Burt (1930: 455) found a "positive correlation to obtain between the relative amount of pecking done, as estimated from types of food eaten, and the amount of modification in a number of characters in the skeleton and feathers." However, the correlation found by Burt was between type rather than amount of pecking done and structure. Acorn Woodpeckers probably spend as much time pecking as other woodpeckers, but they peck solely into relatively "soft" objects: acorns, the bark of living and dead trees, and dead or decaying wood.

Like the majority of picids, Acorn Woodpeckers have relatively short legs with four strong toes and needle sharp claws. The birds perch in a variety of ways and although using postures typical of the family, they perch crosswise more often than most other woodpeckers (Abbot 1930, Trotter 1930). They use typical woodpecker climbing and hitching modes of locomotion on vertical branches and hop along limbs or on flat surfaces.

When flying, Acorn Woodpeckers undulate, alternating wingbeats with pauses when the wings are closed. They are stronger flyers than most other woodpeckers and undulating flight is often not as pronounced as in other species. Bock (1970) has found that Lewis' (*Asyndesmus lewis*) and Acorn Woodpeckers, both flycatching species, have disproportionately large wing areas and therefore small wing loads in comparison to similar-sized woodpeckers. These two species have broad rather than long wings, an adaptation to increase lift and maneuverability at low velocities.

RESEARCH AREAS

Field observations were made from October to December 1966 on two Acorn Woodpecker groups 4 km northwest of Orinda, California (MacRoberts 1970); April to September 1968 on 11 groups at the Hastings Natural History Reservation, Monterey County, California; and October 1971 to August 1974 on about 60 groups at the Hastings Reservation.

The Hastings Reservation is a 781-ha tract located in the Carmel Valley in the northern part of the Santa Lucia Mountains. The Reservation was established in 1937 prior to which it was a cattle ranch.

The reservation ranges from 450 m to 920 m elevation. The summers are hot and dry and the winters wet and cold. Precipitation varies annually from 30 to 107 cm with a 30-year mean of 51 cm. The rainy season is from October to May with little precipitation outside these months. July is the hottest month with an average maximum temperature of about 31°C. January is the coldest month with an average maximum temperature of about 16°C. The winter temperatures regularly fall below freezing and summer temperatures regularly rise to 38°C.

The reservation has been divided into seven plant communities (Griffin MS; on file at the reservation, 1974), five of which are of interest here: mixed evergreen forest, foothill woodland, savanna-grassland, riparian woodland, and chaparral.

Mixed evergreen forest is the most extensive community on the reservation and in the surrounding mountains (Fig. 1). This forest type is characterized by sclerophyll, hardwood trees, predominantly oaks, and an absence of conifers. It tends to occur on north exposures and in shaded canyon bottoms where it grades into riparian woodland and foothill woodland. Mixed evergreen forest is characterized by a combination of Coast Live Oak (*Quercus agrifolia*), California Black Oak (*Q. kelloggii*), Madrone (*Arbutus menziesii*), and more variably relic Valley Oak (*Quercus lobata*). California

FIGURE 1. Mixed evergreen forest, grassland, and riparian woodland.

Laurel (*Umbellularia californica*), Toyon (*Heteromeles arbutifolia*), California Buckeye (*Aesculus californica*), and Holly-leafed Cherry (*Prunus ilicifolia*) are present. Associated understory consists of Poison Oak (*Rhus diversiloba*), Coffeeberry (*Rhamnus californica*), Hollyleaf Redberry (*R. crocea*), currants and gooseberries (*Ribes* spp.), Bracken (*Pteridium aquilinum*), and Cream Bush (*Holodiscus discolor*). Little or no grass cover exists.

Foothill woodland (Figs. 2, 3) is characterized by "a well developed deciduous oak community on the warm dry upland slopes, particularly of

FIGURE 2. Foothill woodland with a small patch of chaparral in left center.

southern exposure" (White 1966a, Griffin MS). This habitat is open enough to have a significant herbaceous cover under and between the trees with perennial grasses (predominantly *Elymus glaucus*, *Poa scabrella*, and *Koeleria macrantha*) and forbs both important. Predominant annuals are *Bromus*, *Avena*, and *Festuca.* Deciduous oaks, primarily Blue Oak (*Quercus douglasii*) but also Valley Oak, are the dominant trees. Foothill woodland varies from widely spaced Blue Oaks in its more "savanna" phase with distinct patches of grassland between the trees and frequent scattered, often solitary Valley Oaks to areas where the oaks grow sufficiently close together to prevent extensive grass development. In this latter "woodland" phase, various shrubs, especially Coffeeberry, Hollyleaf Redberry, and Poison Oak, occur as an understory but are less dense than in mixed evergreen forest.

Foothill woodland grades into savanna-grassland (Fig. 4). Savanna habitat is characterized by widely spaced large Valley and Blue Oaks with a well-developed grass cover and a minimum or lack of shrubby understory. A large portion of the present savanna-grassland communities on the reservation were once cultivated fields. These old-fields probably were formed by eliminating trees from parts of the savanna. Portions of some fields were cleared from mixed evergreen forest (White 1966b, Griffin MS). Old-field systems in which a large portion of the original vegetation has been removed either from foothill woodland or from mixed evergreen forest leaving large mature Valley, Blue, or Coast Live Oaks often abut, in some cases very abruptly,

FIGURE 3. Foothill woodland consisting mainly of Blue Oaks with a large partly dead Valley Oak granary in center.

mixed evergreen forest, foothill woodland, or riparian woodland. Dominant grasses in the savanna-grassland habitat are introduced annuals: *Avena*, *Bromus*, *Aira*, and *Festuca*.

Riparian woodland (Fig. 1) is not extensive on the reservation. The dominant trees are willow (*Salix* spp.), California Sycamore (*Platanus racemosa*), Coast Live Oak, and Valley Oak. California Buckeye occurs particularly along creeks running in narrow, shaded canyons where the plant

FIGURE 4. Savanna-grassland grading into foothill woodland and mixed evergreen forest.

cover is largely an extension of mixed evergreen forest. The understory is Pacific Blackberry (*Rubus ursinus*), Blue Elderberry (*Sambucus mexicanus*), California Wild Rose (*Rosa californica*), currant, gooseberry, and more variably, Coffeeberry. In some areas Poison Oak and Cream Bush occur.

Chaparral (Fig. 2) is characterized by dense stands of Chamise (*Adenostoma fasciculatum*), Coast Ceanothus (*Ceanothus ramulosus*), scattered Manzanita (*Arctostaphyla* spp.), and occasionally California Mountain Mahogany (*Cercocarpus betuloides*).

DISTRIBUTION OF GROUPS AT HASTINGS

Figure 5 shows the distribution of Acorn Woodpecker groups at Hastings and on the surrounding ranches during most of the study. The encircled

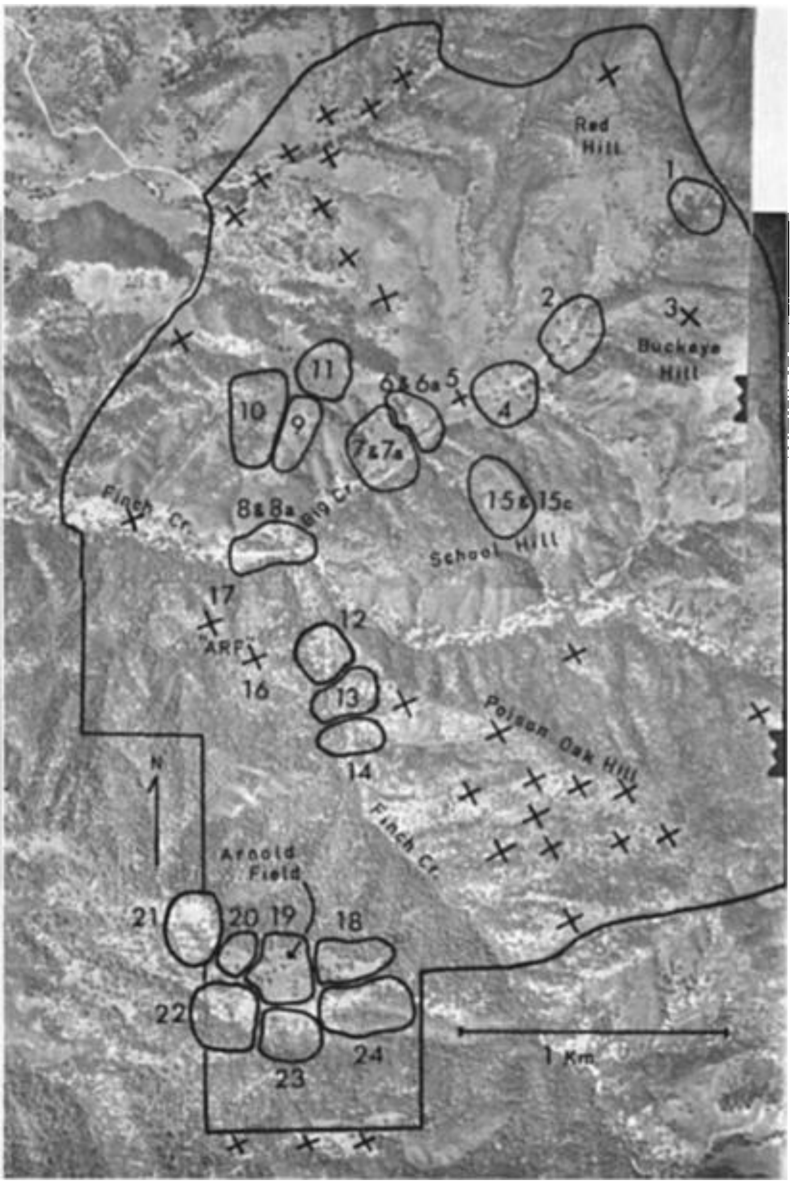


FIGURE 5. Aerial photograph of study area. Encircled areas show approximate group territories. Numbers refer to group designations. Areas marked by an X indicate a group where territory boundary was not known.

TABLE 1

PLANT COMMUNITIES INCLUDED IN ACORN WOODPECKER TERRITORIES

	Community				
	Mixed evergreen forest	Foothill woodland	Chaparral	Riparian woodland	Savanna-grassland
Percent of territories having community	90	95	65	40	85
Percent of territories where community was extensive	35	50	5	35	80
Percent of territories where community was present but not extensive	55	45	60	5	5
Percent of territories where community was absent	10	5	35	60	15

areas represent approximate territorial boundaries; areas marked with an X indicate the presence of groups where the boundaries were not well known.

Table 1 summarizes the types of plant communities included within the territories of the 20 best known groups. Three communities—savanna-grassland, foothill woodland, and riparian woodland—were preferred.

For groups whose territories were not well known the major habitat types were about the same as for the 20 study groups. Groups in the northern end of the study area occupied riparian woodland, foothill woodland, and savanna-grassland; some territories included minor extents of chaparral and mixed evergreen forest. Groups on the southwestern slope of Poison Oak Hill and the one group on Buckeye Hill occupied foothill woodland with, in some cases, small areas of mixed evergreen forest. The four groups on the north slope of Poison Oak Hill and on the Arnold Road Flats ("ARF") lived in foothill woodland "islands" surrounded by dense mixed evergreen forest.

GROUP COMPOSITION

An Acorn Woodpecker group is defined operationally as comprised of those individuals that share a territory. Most groups changed composition during the study. The largest at Hastings numbered 15 individuals. Several consisted of only a pair. The average group numbered between five and six individuals and all groups were bisexual. No individuals lived alone.

Most groups had approximately equal numbers of males and females. Sex ratios for Hastings were calculated in two ways. First, of all birds of known sex banded at Hastings 62 were males and 56 were females (1.1:1). Second, of all birds known in groups at the group's largest size (including unbanded individuals) 87 were males and 71 were females (1.2:1). The Moore Laboratory of Zoology collection at Occidental College contains 246 Acorn Woodpeckers collected in Mexico by R. T. Moore, C. Lamb, and J. Davis. Of these 133 are labeled male and 113 female (1.2:1). The Museum of Vertebrate Zoology contains 177 specimens from California and Oregon that have completed their post-juvenal molt. Of these 95 are males and 82 females (1.2:1).

It is impossible to sex juveniles on plumage characters prior to the post-juvenal molt (Spray and MacRoberts 1975). Of 35 nestlings banded in 1972 and 1973, 20 were seen after post-juvenal molt. Of these 13 were males and 7 were females. Of 13 individuals banded after fledging but before post-juvenal molt, 12 were seen after molt. Of these 4 were males and 8 were females. Because these figures are small, little can be said about a possible bias in juvenile sex ratio.

Combined field and museum data give an overall figure of 315 males and 266 females. The difference is significant in a Chi-squared single sample test ($0.05 > P > 0.02$). Whether differential survival of the sexes or a biased primary sex ratio exist is not known.

Groups are composed of individuals of all ages. However, as group recruitment was largely by reproduction and as many groups at Hastings either did not breed or failed to fledge young, this resulted in some groups that were composed entirely of "old" birds. Others contained individuals fledged before the study began and individuals fledged in each year of the study. The oldest known bird at Hastings was a leucistic male first observed in 1968. He was present on the same territory when the study terminated and was thus at least 6 years old.

Appendix II summarizes group composition and individual life histories.

FOODS AND FEEDING BEHAVIOR

Acorns

Acorns constitute a substantial portion of the woodpeckers' diet. Beal (1911), basing his analysis on the stomach contents of 84 individuals collected in California during all months except February, April, and July, found 23% animal and 77% vegetable matter. Of the total 53% was acorn cotyledons. Neff (1928), on the basis of stomach contents of 72 Acorn Woodpeckers from Oregon collected in every month, found essentially the same proportions of vegetable to animal matter (Table 2). In both samples acorns were present

TABLE 2

STOMACH CONTENTS OF ACORN WOODPECKERS

	Beal (1911) Percent	Neff (1928) Percent
Beetles	2.9	7.3
Ants	8.1	10.4
Other Hymenoptera	7.3	0.5
Other insects	4.5	4.7
Fruit	22.9	1.5
Acorn cotyledons	53.3	59.8
Other vegetable	1.0	15.8

in the diet in all months and formed the largest percentage of stomach contents at all times of year except the summer.

Six oak species and five hybrids among these grow on the Hastings Reservation (Griffin MS). The most common and most important species for the woodpeckers are Coast Live, Valley, and Blue Oaks. The California Black Oak and Canyon Live Oak (*Quercus chrysolepis*) are not widespread on the reservation. Black Oaks are most common at higher elevations and are usually present only in woodpecker territories on hill tops. The Canyon Live Oak is locally common but is not plentiful in most areas inhabited by the woodpeckers. The Shrub Live Oak (*Q. turbinella*) is also locally common but does not appear to be important in the economy of the Acorn Woodpecker at Hastings.

Table 3 shows the oak species present on the territories of the twenty groups where boundaries were best known. All groups at Hastings had access to at least three oak species and some groups had as many as five within their territories. Except when the acorn crop is very poor or patchy, circumstances that will be discussed later, each group harvests acorns exclusively within their territory.

The woodpeckers eat the acorns of all oak species. As the nuts vary in size both within and among species and also in some aspects of morphology among species, the birds employ various techniques in handling them. Black and Canyon Live Oaks generally produce the largest acorns although some Valley and Blue Oak acorns are as large or larger. Typically Coast Live and Blue Oak acorns are smaller than acorns of the other species.

From late summer through autumn the woodpeckers feed on green acorns. The time at which this begins depends on the development of the nut crop. The earliest nuts taken are from Black Oaks, which develop 2 to 3 weeks in advance of the other species. When the acorns ripen the woodpeckers cease eating all they pick and begin storing, although they continue feeding on green nuts through the storage season.

TABLE 3

OCCURRENCE OF OAK SPECIES ON HASTINGS ACORN WOODPECKER TERRITORIES

	Oak species				
	Coast Live	California Black	Valley	Blue	Canyon Live
Percent of groups with oak present on territory	100	60	100	100	50
Percent of groups where oak was common	100	15	100	95	25
Percent of groups where oak was uncommon	0	45	0	5	25
Percent of groups where oak was absent	0	40	0	0	50

The methods used for picking vary with oak species and state of maturity of the nut. Mature nuts are easily picked because just before they fall they loosen in their cups and may be virtually free. The birds typically pick acorns directly from the trees, hanging "chickadee" fashion among the terminal branches. An acorn is grasped in the mandibles by the pointed end, bent toward the body, and twisted. This usually frees the nut from its cup.

Before the acorns mature the woodpeckers often have difficulty picking them. Black Oak acorns are probably the easiest to pick in the immature state. They are attached to the limb by short, brittle stems and grow on larger branches than do the acorns of other oak species. The woodpeckers pick these nuts by grasping their stems in the bill and bending them. Because the acorns of other species grow on flimsier branches, the birds usually must hang in awkward positions to pick them. In these cases a bird grasps an acorn as when picking mature nuts and then bends it. This may free it, sometimes with stem, cap, and surrounding leaves attached. If the nut does not come free, the bird may pull off the surrounding leaves and peck at the stem near the base of the cup. The acorn is again grasped in the bill and twisted. These maneuvers may be repeated several times before the nut breaks free. If the acorn proves particularly difficult, it is abandoned.

Acorns are seldom picked up from the ground. This occcurs most commonly when a woodpecker drops a nut.

The birds carry acorns primarily in two ways depending on how they are picked. If picked by the stem, they are carried by the stem. If a nut is picked by grasping it in the mandibles, it is carried in this manner held length-

FIGURE 6. Carrying acorn blunt (cap) end out.

wise, blunt or cap end outward (Fig. 6). Only rarely are acorns carried crosswise in the bill.

Acorns are worked at anvils. These are special locations on the upper surfaces of horizontal or nearly horizontal limbs where cracks and crevices provide a suitable "hold-fast" (Fig. 7). Such sites may be the nearly flat, partially rotted tops of utility poles or any other location where a nut can be secured from rolling. Unlike corvids, Acorn Woodpeckers do not use their feet to steady acorns and such hold-fasts are essential. Anvils are used to prepare nuts for consumption and for storage.

Acorns tend to be opened in two ways depending on their state of maturity. The birds usually open immature nuts that still adhere tightly to the cap in the following manner. A bird carries the nut to an anvil and lays it lengthwise in front of itself. The cap may be directed either toward or away from the

FIGURE 7. Opening acorn at anvil.

bird. The acorn is placed on the anvil at a level with the bird or slightly above it. The bird then moves to a position with its head directly over the nut and directs "power" pecks along the midline of the acorn. This type of pecking involves whole body movement with the tail firmly braced and the legs generally greatly extended; head and body are raised above the nut, and by quickly flexing downward the bird drives its bill into the acorn. The head moves in a wider arc than the body. Power pecking is used to break through the shell and to de-cap acorns. After the initial cut is made, a piece of shell is chiselled out to one side of the cut exposing the cotyledons. Sometimes two parallel cuts are made and the shell between them is removed. California Black Oak acorns are the most difficult for the birds to open. Their shells are tougher than the shells of other acorns and breaking through often requires more pecking (Fig. 8).

When opening acorns that are nearly mature but that have the cap attached, the birds use another method. The nut is laid on an anvil as described above and power pecks are directed at the cap. The nut may pop free on the first peck or a chip may flake off from the cap. If the chip comes free, the nut may then fall loose. If it does not, the bird either continues to peck at the cap-nut juncture or open the nut by pecking at it in the area exposed by the removal

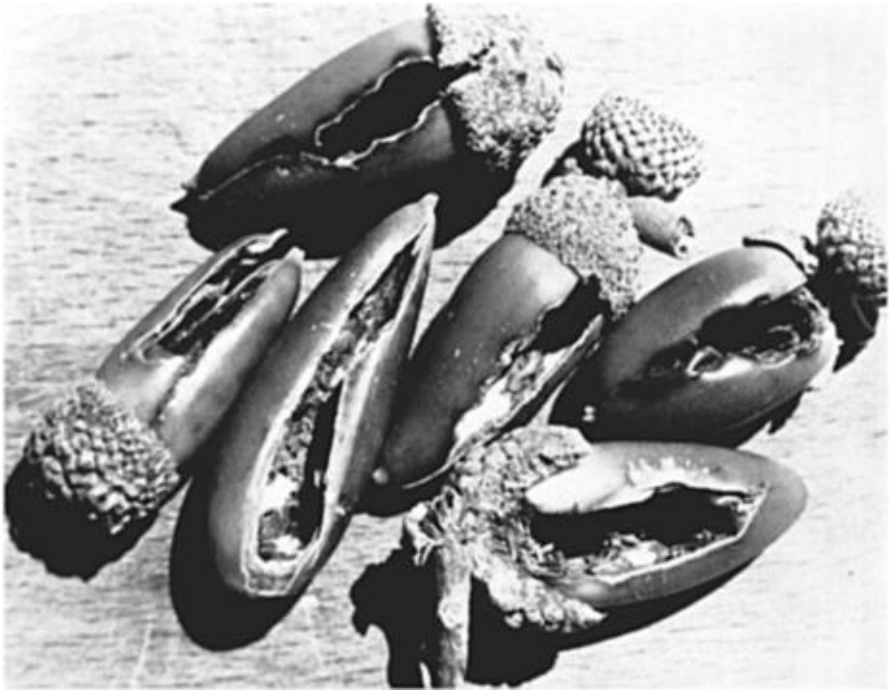


FIGURE 8. Immature Valley Oak acorns opened by Acorn Woodpeckers.

of the chip. Once the nut has been de-capped, it is aligned lengthwise in front of the body and with power pecks the bill is driven through the shell and into the cotyledons in one or several places along the midline. With the bill inside the nut, a bird twists its head in a series of peck-twist-twist-peck-twist movements that split the acorn into two neat halves (Fig. 9). This method is used to open mature green nuts and stored dried acorns.

Once a nut has been opened, either by splitting it or by opening one side, the bird changes pecking procedure to remove the cotyledons. This "precision" pecking mainly involves head movement in which the bill may be slightly opened. Body flexion is less pronounced than in power pecking, although the bird may use power pecks to dislodge the cotyledons and precision pecking to break them up.

If the acorn has been opened by chiselling a hole in it, the cotyledons are eaten directly from the shell. If the nut has been split lengthwise, the cotyledons may be removed from the shell before they are broken up. This is done in a number of ways but two are most commonly used. A bird carries half of the acorn to another anvil, places it base end downward in a crack, and pecks at the cotyledon-shell juncture near the tip of the nut. This pops

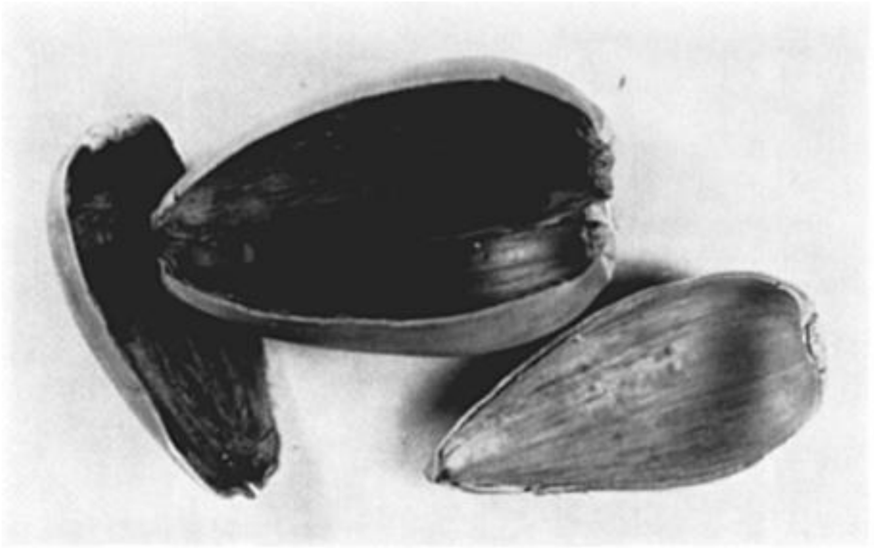


FIGURE 9. Mature Valley Oak acorns split longitudinally.

the nut meat free. Or the bird places the nut on its side and with a similar procedure removes the nut meat.

Cotyledons generally are eaten at the anvil where they have been opened, but they may be taken to another anvil for consumption. Empty shells and caps are often left at anvils, as are half-eaten nuts and halved acorns with cotyledons still in place. Whole nuts may also be left. A bird either eats from an opened nut and leaves the remainder, splits the nut and carries half elsewhere to eat, or brings two nuts simultaneously to an anvil, separates them

TABLE 4

DIMENSIONS AND FREQUENCY (IN PERCENT) OF GRANARIES AT HASTINGS

Granary type	Number of observations	Average dbh (range) in m	Average height (range) in m	Percent of granaries
Valley Oak	88	0.99 (0.28–1.53)	14.5 (2.4–24.0)[1]	78
Blue Oak	17	0.65 (0.28–.90)	11.5 (3.05–18.3)[1]	15
Sycamore	5	0.74 (0.36–1.28)	16.4 (9.6–24.0)	4
Black Oak	2	0.62 (0.48–.76)	13.5 (12.0–15.0)	2
Willow	1	0.50	12.0	1

[1] The minimum heights for Valley and Blue Oaks refer to trees with broken tops.

FIGURE 10. Sycamore granary at Toro Park, Monterey County, California.

from the attached stem, and carries one to another anvil to work it. The next bird to arrive at the anvil cleans up before beginning to work its acorn by simply throwing overboard the accumulated shells and caps. If whole or partly eaten acorns have been left, it may abandon its nut and work these.

Within the boundaries of each group's territory there are one or more granaries, usually large, somewhat isolated trees. At Hastings, trees used

FIGURE 11. Oak fence post used as granary.

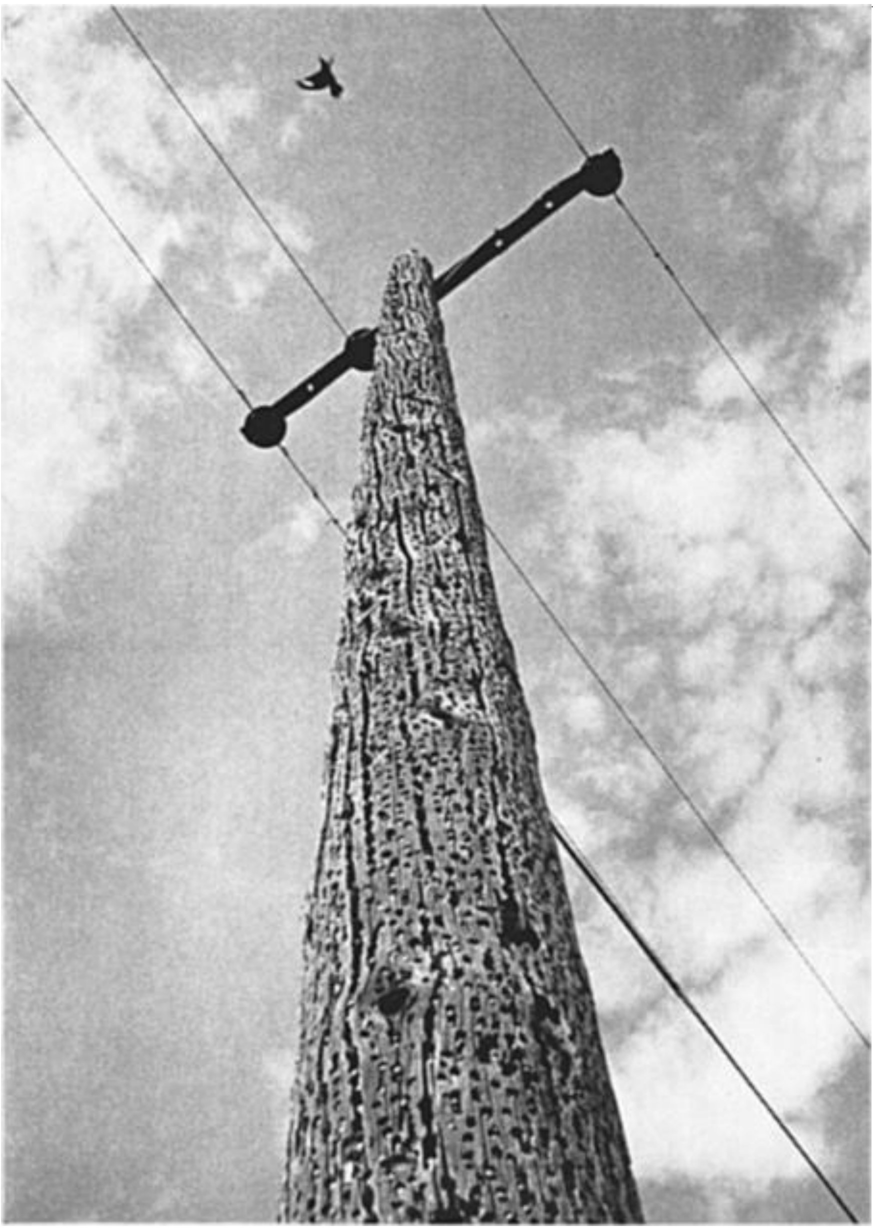


FIGURE 12. Utility pole near Carmel Valley, California, used as granary.

FIGURE 13 (Left). Acorn Woodpecker storing an acorn. Note arrangement of acorns in storage limb and the way the woodpecker is carrying the acorn.

FIGURE 14 (Right). Storage limb from Hastings with Coast Live Oak acorns (left) compared with storage limb from Cone Peak, Monterey County, containing Tanoak acorns. Scale in cm.

as granaries were Valley, Black, and Blue Oaks, sycamores, and willows. Information concerning the types of trees used as granaries and their dimensions for 53 groups appears in Table 4. In addition to trees, utility poles or fence posts are used occasionally (Figs. 10, 11, 12; see also photographs in Ritter 1938, MacRoberts 1974). For the 53 groups sampled, the average number of granaries was 2.1 with a maximum of seven on one territory.

Other types of granaries have been noted in the literature: various pines (*Pinus* spp.), firs (*Abies* spp.), Redwoods (*Sequoia sempervirens*), and eucalyptus (*Globulus* spp.). But almost any dead tree or trees with fairly deep dry bark, or even buildings, may be used (Ritter 1938).

Storage holes vary in size according to the type of acorn being stored, but have a standard shape. Holes have a circular entrance that narrows slightly just below the surface. Beyond this neck, the cavity gradually widens and is widest toward the base. Holes are drilled straight into the bark or wood and their arrangement varies with the surface in which they are excavated. On smooth surfaces with no desiccation cracks, the typical arrangement can be seen in Figure 13: a "Chinese checker" pattern. In deep, crenelated bark such as that of mature Valley Oaks and sycamores the holes are made mainly on the raised plateaus and not in the furrows between. Storage holes may follow desiccation cracks as widenings of the cracks and their pattern in this case follows the cracks, one hole above the other. The spacing of storage holes depends additionally on their size. Large holes are more widely spaced than small holes (Fig. 14). Holes generally are drilled only into dry bark or dead wood and rarely penetrate into the living part of the tree.

The largest number of functional storage holes on any one territory at Hastings was estimated to be about 11,000 in two granaries taken together. The average number of storage holes for a group at Hastings was about 4100 based on a sample of 26 groups.

The construction of a granary is the work of generations of woodpeckers. The majority of holes in a given territory are the result of hole-making in previous years. The birds do not make a single hole, then store in it before making another, but use existing holes year after year, adding new ones each year.

Drilling new storage holes takes place mainly during the latter part of the storage season and continues through the winter months. In the storage season itself the birds devote considerable time to refurbishing old holes by pecking out the empty shells remaining from the previous year and enlarging and deepening the holes. Construction of storage holes is time-consuming, and it is rare that a single individual makes a storage hole at one sitting. Typically a particular hole is drilled over several days by several individuals.

Storage holes are begun by chiselling out a *V*-shaped wedge. When the *V* is completed, the inside portion is expanded by pecking at an angle into the wedge (Fig. 15). Holes are about 30 to 40 mm deep or approximately the limit of the bird's bill. The time required to make a hole depends on the substrate used; soft bark or dead, partially rotted wood are the most easily excavated. For one sample, storage hole construction into the bark of a Valley Oak ranged from 30 to 60 min of continuous work.

At Hastings each group probably added only a few hundred holes each year. Some of this work only canceled out losses: branches with storage holes fall and become useless and other holes become derelict through expansion caused by growth of the trees.

All members of the group, except in some cases first-year birds, appear to participate in storage hole construction. We noted no division of labor.

Acorn Woodpeckers store nuts other than acorns when these are available. Among these are almonds, walnuts, hazelnuts, and pecans (Ritter 1938, Bent 1939). We can make only two additions to this list. Digger Pine nuts (*Pinus sabiniana*) were stored on a large scale by one group on the Hunter Liggett

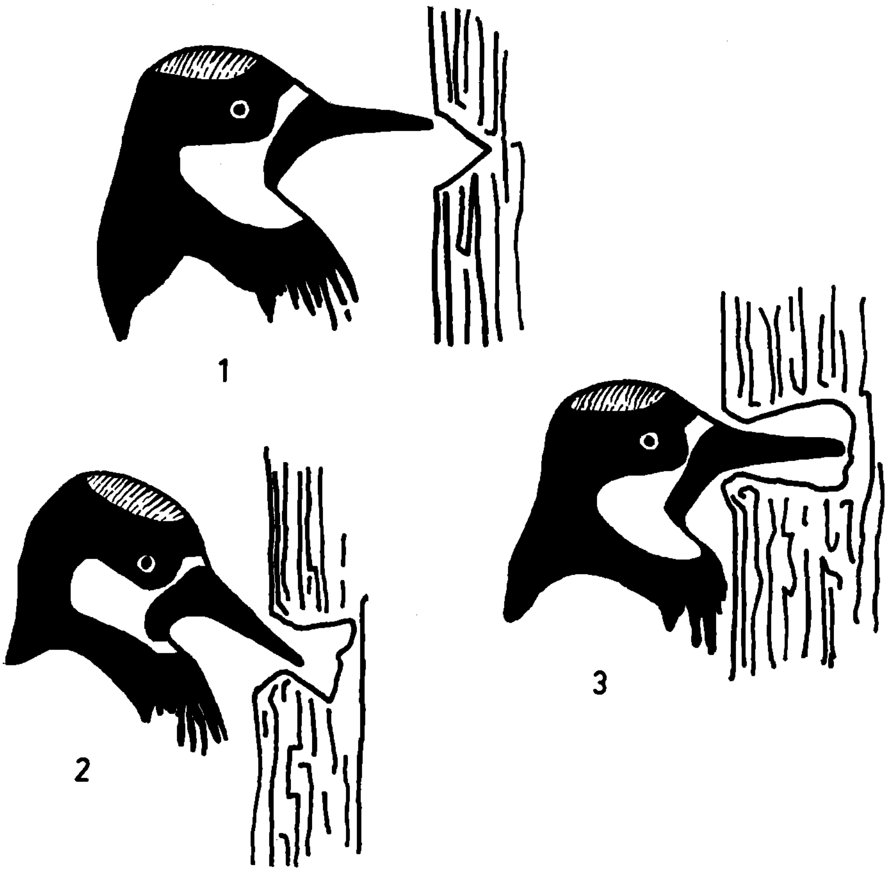


FIGURE 15. Storage hole construction showing shape of hole in cross-section.

Military Reservation, Monterey County (Fig. 16). Tanoak acorns (*Lithocarpus densiflora*) were stored in Sugar Pines (*Pinus lambertiana*) on Cone Peak, Monterey County. At Hastings only *Quercus* acorns were stored.

Acorn storing begins just before the nuts are ready to fall from the oaks. The birds pick and carry the acorns in the manner described previously. Nuts are carried to a anvil, laid down, and the direction of carriage reversed. If the cap still adheres, it is removed before storing. The nut is carried, now with the pointed end outward, to a granary where the bird searches for a hole of suitable size. It passes up some but pauses at others and touches the nut to the hole. When a suitable hole is found, the bird presses the nut into it while simultaneously backing its bill away keeping the nut in place the while. Then it pounds the nut into the hole. If the hole is the correct size, pounding

Figure 16. Digger Pine nuts and acorns stored in Digger Pine, Hunter Liggett Military Reservation, Monterey County.

drives the acorn snugly below the surface. Almost all acorns are stored blunt end outward.

After the nut is pounded in, the bird may test its security by alternately pecking on the base, the margin of insertion between it and the wood, or at the side of the nut if the base protrudes from the hole. The bird may regrasp the nut and attempt to pull it out or may even stick its tongue into the gap between the acorn and the hole and jiggle the nut around. If the acorn does not fit, that is, if it meets resistance and does not pound down or if it is loose in the socket, the bird extracts it. It may attempt to store the acorn again in the same hole, rotating the nut slightly before reinserting it. If this does not produce the desired fit, the nut is carried to another storage hole.

The woodpeckers are adept in handling nuts. After picking an acorn for storing, they do not always use an anvil to reverse the direction of carriage. Instead they may carry the nut directly to the granary, blunt end outward, and reverse it without laying it down. A bird holds the nut in its bill and perching vertically, presses the nut against the tree directly in front of it. By putting pressure on the acorn as it is pressed against the tree, the bird swivels it into a crosswise position in its bill. Holding it firmly horizontal to the tree, it then moves its head around the blunt end of the acorn and reverses it so that the pointed end is outward and the nut can be stored.

While storing, if a bird loses control of an acorn, it quickly drops its wrists and breast to the branch and catches the nut in the pocket thus formed. If the nut falls, the bird may fly after it and occasionally catches it before it hits the ground.

It is clear that the birds can judge rather accurately the size of acorns to be stored and generally store only in holes of about the correct size. Sometimes this is uncanny. We observed a female refurbishing a storage hole. She had enlarged the entrance slightly and had cleared some shell from it. She flew to a Black Oak and soon returned with an acorn. She landed at an anvil, reversed the nut, and flew directly to the refurbished hole. She placed the nut in the hole and began pounding. The acorn went in about half way; she paused and then gave another series of pecks at the nut, which like a nail slowly sank below the surface until it was slightly countersunk—a perfect fit. She then flew off to fetch another nut without testing its security, leaving one wondering if, while selecting the acorn, she had had the recently cleaned hole in view and picked the nut specifically to fit it! This however is not the typical pattern, and the woodpeckers usually try several storage holes before finding one of the correct size.

The woodpeckers sometimes show behaviors that result in the loss of acorns. They occasionally store nuts in places from which they cannot retrieve them, as when storing in trees in which the heart wood has rotted leaving a hollow. In one instance, a group used a hollow limb with a series of desiccation cracks for storage. The birds repeatedly jammed nuts into the oversized cracks, only to have them fall inside the tree. However, about 3 m below the cracks was a large knot hole, and the birds soon learned that if they lost a nut they could enter this hole and retrieve it. On one occasion,

FIGURE 17. Acorns stored under tiles at Mission San Antonio de Padua.

a bird stored one nut seven times in succcession in the same place before it gave up and stored the nut elsewhere. All such situations do not lead to eventual success: Peck (1921) records "I have seen a hollow pine tree with a cavity six to eight inches in diameter filled for a distance of nearly twenty feet with acorns dropped into a good sized hole at that distance above the ground. An opening at the bottom showed the earlier acorns deposited, completely decayed and crumbled to dust."

When the woodpeckers first begin storing each year, they store whole acorns in prepared holes; but as the season wears on they begin storing whole nuts, halved nuts, and pieces of mast in natural cracks and crevices. They often fill abandoned roost holes with whole nuts or they wedge whole acorns into the deep furrows of Valley Oak bark. They store halved nuts, either with shell adhering or with cotyledons removed, mainly in the granaries, but also insert them into desiccation cracks and into fissures in bark, under loose bark, or even under roofing shakes. One group stored acorn pieces in one of our blinds. At Mission San Antonio de Padua near Jolon, California, we observed a group storing under the tiles on the mission roof (Fig. 17).

When storing halved nuts, a bird splits the nut, carries half away and stores it, and generally returns immediately to the anvil and retrieves the other half. However, temporarily abandoned halves may be eaten or taken away and stored by another member of the group.

The storage of acorn halves and pieces occurs mainly in the latter part of the storage season. Presumably as storage holes are filled, the only remaining way to store is to break up the nuts and store them in places that are not suitable for whole acorns. This obviously increases the amount of food laid away, but it is difficult to estimate by how much.

As acorns dry they shrink, and nuts that originally fitted their receptacles soon become loose. In a period of 2 weeks the diameter of acorns shrinks about 6%—a figure based on a sample measured for this purpose. Because of shrinkage, an acorn may be moved several times before it is permanently left in place. Throughout the storing season and continuing for some time after the last acorn has been gathered, the woodpeckers spend considerable time rearranging the stores.

Stored acorns are the woodpeckers' major food through the winter and on some days their only food. However, if stored nuts are available they are eaten throughout the year. Under certain conditions nestlings are fed acorn meat. Apparently the use of stored acorns in summer and their use as food for nestlings is related to availability of other foods, particularly insects. On days when coastal fog blanketed the area and temperatures were low, groups with acorns fed on them until the fog lifted and insects became available.

The methods for preparing stored acorns for consumption are somewhat different from those used in dealing with green nuts. Typically the birds use two methods for extracting the cotyledons. If an acorn is loose in its storage hole, it is simply removed, taken to an anvil and split open. When nuts are so tightly wedged in that they cannot be removed, the birds do not peck the nut free by removing surrounding wood, thereby destroying the storage hole, but instead peck out the exposed base of the nut. The cotyledons are then removed or eaten *in situ*. If removed, the cotyledons are taken to an anvil and broken into swallowable bits. Pieces not eaten may be re-stored. When the nut meat is eaten *in situ*, a bird clings to the tree with the head level to the nut and pecks out small pieces. The nut may be left partially eaten, in which case other group members may eat the remainder or the bits and pieces are restored. As whole acorn stores are depleted, the woodpeckers glean for these re-stored bits. Long after a granary looks empty, the birds continue to feed on re-stored fragments. When anvils are covered with snow, the woodpeckers eat all acorns *in situ*.

At Hastings most groups exhausted their acorn stores by spring. Few groups had acorns left into the summer and all had exhausted their stores by the time storing began the following year.

The habit of storing acorns in prepared holes does not characterize the Acorn Woodpecker over its entire range. In the United States and Mexico the use of prepared holes is common (Fuertes 1903, Huey 1926, Ritter 1938, Bent 1939, Goldman 1951, Walker 1952, Blake 1953). In Central America in some localities Acorn Woodpeckers store acorns in prepared holes (Salvin 1876, Peck 1921, Eisenmann 1946, Russell 1964, Wetmore 1968, Skutch 1969, Howell 1972), but in others they do not store at all or store only in cracks and crevices (Dickey and van Rossem 1938, Skutch 1969). In some parts of its Colombian range, the Acorn Woodpecker stores in the manner typical of more northern birds (Miller 1963). In Miller's unpublished South American field notes on file in the Museum of Vertebrate Zoology, the following passages are of interest here. "Stands of tall oaks. *Balanosphyra* was common, congregating in family groups or tribes in the occasional dead tree. Here were a few acorn holes but not conspicuous spreads" (28 September, 15 km north Popayan, 5800 feet, Cauca, Colombia). Later in the notes Miller writes: "*Balanosphyra formicivorus* was found in some dead cecropias standing in the northern pasture pocket. Here were 6 + nest holes and a few small storage holes that looked empty" (21 December, Rio Anchicaya, 1500 feet, Valle, Colombia). These are the only references that we have been able to locate that indicate that this species stores in prepared holes in Colombia. Other reports indicate that in this region Acorn Woodpeckers do not store acorns (K. von Sneidern pers. comm.).

It appears that the habit of storing in prepared holes characterizes the species over most of its range but that in Central America and Colombia the habit is met with in some localities only. It should be remembered that the birds store acorns in two ways in the northern part of their range—in prepared holes and in cracks and crevices. It may be that in those areas for which storage has not been reported, the birds store in the latter places only. This type of storing is more difficult to detect by casual observation. Yet it remains highly probable that in some localities the Acorn Woodpecker does not store.

SAP

Many species visit the bleeding areas of a tree and eat the exudations, but few make holes for this specific purpose, that is open the bark in such a manner that sap runs into the damaged area. Yellow-bellied Sapsuckers are notorious for this behavior (McAtee 1911, Tate 1973). According to Tate (1973) sapsuckers eat "all of the soft inner bark-cork cambium, phloem . . . , and cambium . . . as well as the sap associated with it." This is called "bast." Other woodpeckers that make sap holes are the Red-headed Woodpecker (*Melanerpes erythrocephalus*) (White 1873, Kilham 1959), the Great Spotted Woodpecker (*Dendrocopos major*) (Witherby et al. 1948), and the Acorn Woodpecker (MacRoberts 1970).

Several early observers refer to the sap-eating propensities of the Acorn Woodpecker (F. Stephens *in* Bendire 1895: 115; Grinnell 1908: 65–66; Grinnell and Storer 1924: 339–340). Yet it is unclear from these references whether the Acorn Woodpeckers were responsible for making the holes. The latter two references assume that the holes were the work of sapsuckers; Stephens assumed that the Acorn Woodpeckers made them.

At Hastings in 1968 we found evidence that this species drills small holes into the bark of Coast Live Oaks and eats the sap from them (MacRoberts 1970). Upon resuming observations in 1971 we found that sap eating begins each year in late January or early February. At this time the woodpeckers frequent old sap borings to refurbish them and to add new holes. Sap eating is rare however until late February or early March.

FIGURE 18 (Left). Tanoak sap tree, Cone Peak, Monterey County. Dbh about 20 cm.
FIGURE 19 (Right). Detail of Tanoak sap tree.

Each group has within its territory several localized areas where borings are made. The same holes are used each year with a few new ones added. Sap hole construction is a communal affair and all members of the group use them.

The woodpeckers at Hastings confine sap eating to oaks. We have observed them making holes in and eating sap from Black, Blue, Valley, and Coast Live Oaks. On Cone Peak, Monterey County, we found one magnificent Tanoak that was literally pockmarked from top to bottom with Acorn Woodpecker sap holes (Figs. 18, 19).

At any particular time each group has several localities where it obtains sap. One group may be eating sap from Coast Live Oaks while a neighboring group is eating sap exclusively from Blue Oaks. Why this should be is not obvious, but it indicates that at any given period when sap is eaten, different oaks are equally suitable. Additionally as the season progresses each group switches sap eating from one location to another. For example, in February the birds of one group ate sap from a Valley Oak for about a month and then switched to a Coast Live Oak and a Blue Oak that they used for the remainder of the season.

Sap eating is common from late winter through summer, when the birds begin eating green acorns. In 1972 the woodpeckers began sap eating in February and March and continued to early October. The following year they began at the same time but stopped in late August, about 5 weeks earlier than in the previous year. The difference appeared to be related to an early nut crop in 1973 and therefore an earlier resumption of feeding on acorns.

Acorn Woodpecker sap holes are easily distinguishable from sapsucker holes, which are smaller, more closely spaced, and which often girdle the tree. Sap holes are smaller in diameter and shallower than acorn storage holes but the spacing pattern is similar. Sap holes measure 5 to 15 mm in diameter and 3 to 19 mm deep. They are usually excavated on the upper surfaces of middle and upper canopy limbs. Holes may be made on vertical limbs. They are drilled to the wood but not into it and tend to be made in branches measuring 2 to 15 cm in diameter. Diameter and depth of sap holes correlate with diameter of the limb used and with bark depth; larger limbs support wider and deeper holes. During the height of the sap-eating period each hole is visited about 4 to 10 times per hour.

No competition at Hastings between Yellow-bellied Sapsuckers and Acorn Woodpeckers was noted. Sapsuckers are migratory, arriving in the autumn and leaving in the spring. We saw an occasional sapsucker at Acorn Woodpecker borings, but this was usually in the autumn after the woodpeckers had ceased eating sap.

Neither Beal (1911) nor Neff (1928) mentions bast or sap as part of the stomach contents of Acorn Woodpeckers, although they record large quantities of bast in the stomachs of sapsuckers. It appears therefore that the Acorn Woodpecker does not eat bast at all but only sap. This would explain why Acorn Woodpeckers make so few sap holes even when a large group is feeding from them.

INSECTS

Both Beal (1911) and Neff (1928) found 23% insects in the stomach contents of the Acorn Woodpeckers in their samples; insects were taken mainly in spring and summer.

Acorn Woodpeckers are primarily flycatchers and only occasionally glean or dig into wood for insects and their larvae. Flycatching is characteristic of the species over its entire range and has been recorded for many localities from Oregon to Colombia (Walker 1952, Miller 1963, Skutch 1969). This activity is not limited to any particular season but is most common in spring and summer. Rate and occurrence of flycatching are probably related to the presence and relative abundance of slow flying insects, mainly beetles and Hymenoptera.

The Acorn Woodpecker also stores insects. When flying insects are abundant the birds make repeated sorties, capturing prey items as fast as possible and pausing only to jam them into a crack or crevice between flights (Walker 1952, MacRoberts 1970).

Following Bock's (1970) classification, flycatching may be divided into two types: (1) nonspecific flights in which a bird catches several prey items before returning to a perch and (2) specific flights in which a bird catches a single insect during a sortie. Probably about 95% of all sorties observed at Hastings were specific flights, but on some days we observed up to 25% nonspecific flights.

When flycatching, the woodpeckers usually perch on any high, exposed point where the view is not obstructed. They scan by moving their heads from one fixed position to another. More rarely a bird may "steady track" by moving the head slowly and uninterruptedly.

Typically a woodpecker does not orient directly at the prey before flight. Once an insect is sighted, the bird flies and then corrects direction. If an insect is over 90° from the direction in which a bird is facing, it may quickly hop to a position facing the insect and then fly.

The majority of sorties are in an upward direction, sometimes almost vertical. Occasionally flights are downward just above the ground, and more rarely individuals fly down, hover above the grass, and drop on the prey, actually landing.

A woodpecker does one of several things with the prey. A bird may swallow the insect before returning to the perch, return with the insect and eat it immediately, prepare the insect and then eat it, or store it. Large insects are usually taken to an anvil and dismembered by pounding them and pulling off the wings or rubbing them against branches. When storing insects, a bird merely jams them into small cracks or old storage holes, which suitably crushes them. When feeding nestlings, a bird sometimes retains each captured item in the bill; once several insects have been caught, the entire mass is taken to the nest.

The woodpeckers sometimes catch bees. A bird sits close to the hive entrance and either makes short sorties in which it takes bees hovering near the entrance or it sits close to the hive and grabs bees as they land. Bees flying close by may be picked out of the air.

Hawking flights may last up to 43 sec and may take a bird 50 m from its perch. Flights generally begin and end at the same perch. On 3 days we timed 191 specific flights, which ranged from 1 to 22 sec per round trip. The three sets averaged 3, 4.2, and 6.5 sec. On 2 days we timed 52 nonspecific flights, which ranged from 3 to 43 sec and averaged 7.6 and 16.5 sec for the two samples. Acorn Woodpecker sorties are much shorter than those made by Lewis' Woodpeckers (Bock 1970); Bock found that 677 timed flights averaged 16.5 sec with a range of 2 to 480 sec. He combined both specific and nonspecific flights, but the difference is clear. We calculated the success rate of flycatching on several occasions, the criterion being actual sight of the insect when caught or brought back to the perch. The observations are therefore biased on the side of failure. Yet even with this bias, the success rate in eight independent samples involving 121 flights ranged from 60 to 100%.

At the highest rate a bird makes up to six sorties per minute. However, this is rare and sorties in this case are short, lasting from 1 to 6 sec. More generally the rate during good flycatching periods is one flight every 1 to 2 min with most time spent scanning.

When flycatching, individuals may scatter over the territory, but more often several birds hawk insects from the same tree. Occasionally a woodpecker and a bird of another species try for the same insects; this happens with Western Bluebirds (*Sialia mexicana*) and with Scrub Jays (*Aphelocoma coerulescens*). The first to arrive takes the prey, but when two Acorn Woodpeckers simultaneously fly at the same insect, one usually drops back.

We saw little interspecific competition at Hastings for the insects that occur in the niche the woodpeckers exploit. Scrub Jays, Yellow-billed Magpies (*Pica nuttalli*), Western Bluebirds, and more rarely, sapsuckers hawk in the same air space but, with the exception of the bluebirds, these species do so only when insects are very abundant.

When insects are especially abundant the woodpeckers store a large proportion. One female, which we watched carefully, made 14 flights in 10 min, of which 12 were successful; she stored 11 insects and ate 1. On another occasion this same bird made 10 flights in about 12 min, missed 1 insect and caught 9, all of which she stored.

Each bird tends to store insects in a particular place close to its hawking perch, but occasionally several members of the group store in the same place. These larders are not the private property of the individuals that make them. One bird may store insects, another take them and re-store them, and a third eat them. One bird may capture and cache insects and another take them to the nestlings. Stored insects are usually eaten within hours of being cached, but once we saw insects stored one afternoon still being eaten the following morning.

Insect storage undoubtedly increases the amount of food taken. When insects are abundant they can be captured and stored rapidly. In some cases this would shorten the time between each capture by leaving out the steps necessary to prepare the insect for eating. Insect storing, like acorn storing, makes a temporarily abundant food source that cannot be immediately consumed available for a longer period of time. Bock (1970: 38) has suggested that insect caching by Lewis' Woodpeckers during the nestling period "would increase the ability of Lewis' woodpeckers to capitalize upon a temporarily superabundant food source by shortening the time between each capture." This suggestion seems applicable to Acorn Woodpeckers as well.

Unlike other arboreal woodpeckers, Acorn Woodpeckers seldom glean for insects or bore into wood for insects and larvae. As they often glean acorn fragments stored in cracks and fissures, we had difficulty in determining whether a bird was always gleaning acorn bits or was in fact taking insects. They occasionally gleaned areas where acorns were not stored, but when we examined these surfaces we found no evidence of insects. On one occasion we observed the birds of one group enlarge already existing openings in bee or ant galleries. This was the only instance we saw of boring for insects.

The woodpeckers occasionally scaled off pieces of lichen and moss from the upper surfaces of large branches of oaks. This involves pecking under the plants, apparently loosening them, and then tearing away sections with the bill. The torn pieces are then tossed aside. This behavior was not common, and we were never able to determine whether the birds recovered any food as a consequence.

OATS

The woodpeckers sometimes eat oat seeds. For some time we thought they were catching low-flying insects, but we eventually were able to distinguish oat-picking sorties from flycatching by the shorter duration of the flights and by the fact that the birds often flew repeatedly to the same place. When flycatching near the ground, they rarely hover at one place but make continuous swooping flights. When oat picking, the birds sit on low perches, between 1 and 4 m above the ground, and fly out in short sorties. They hover just above the grass stalks, pick off a fruit, and quickly fly back to the perch to husk it. Once we were aware of what the birds were doing, we observed oat picking several times. Oats do not appear to constitute an important item in the diet and are of course confined to midsummer when grain is ripe and ready to fall. We never saw the woodpeckers store grass seeds.

FLOWERS AND LEAVES

Ritter (1938: 28) states "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 I have never been quite certain." This behavior was common at Hastings, and it is clear that the woodpeckers eat oak catkins and perhaps also leaf buds and pistilate flowers. The catkins are sometimes carried to anvils, pounded on, and then eaten. The woodpeckers took catkins from Valley and Blue Oaks in particular.

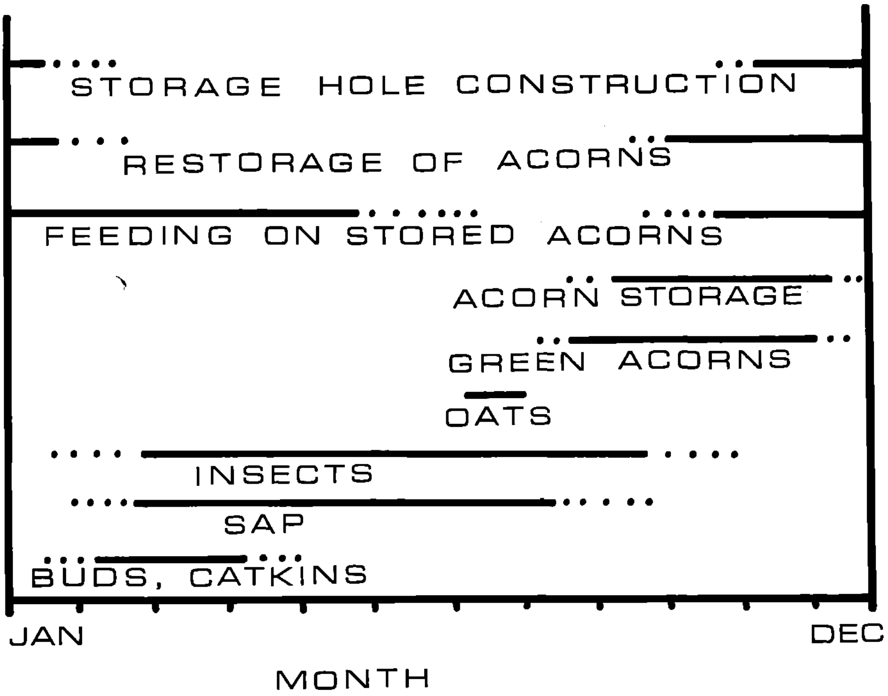


FIGURE 20. Annual food cycle of Acorn Woodpeckers at Hastings.

FRUIT

Like many birds, Acorn Woodpeckers eat fruit if it is available. At Hastings we never observed them taking wild fruit, but in 1973 a pear tree produced a good crop and the birds in one group whose territory encompassed this tree frequently ate the fruit. They did not pick the pears and carry them off but perched next to fruit that hung close to branches, pecked holes in them, and ate out the insides. The birds ate from only a few pears rather than pecking into several. Pear eating continued for some weeks during the summer before most of the fruit were fully ripe.

GRIT

The woodpeckers go to the ground several times each day for grit. They tend to do this as a group. Grit is taken at specific localities, often from road beds. The birds may spend up to a minute hopping about picking up very small rocks. Neff (1928: 46) states that "nearly every stomach was found to contain a large quantity of grit, and some held nothing else." Grit constituted about half the total stomach contents of Neff's sample, which is the largest percentage for any of the woodpecker species examined.

Summary of Acorn Woodpecker Feeding Habits

We conclude on the basis of the present study and the information contained in the literature that Acorn Woodpeckers feed mainly on three foods. They store and eat acorns, they catch insects on the wing, and they eat sap. They do not often glean and almost never bore into wood for insects. Figure 20 summarizes the annual food cycle of the Acorn Woodpeckers at Hastings.

Our study further indicates that much communality exists in the feeding habits of this species. Each group member does not make its own cache of acorns and feed exclusively on them, but all group members (birds of the year excepted in some cases) aid in laying in the stores and all feed on them. All members aid in making new storage holes. Insect caches and sap areas are treated as community property. All group members participate in making sap holes and all feed at them.

SPACING AND SPACE RELATED BEHAVIOR

Noble (1939) defined territory as "a defended area." Pitelka (1959: 253) defined territory as "an exclusive area." The latter definition is preferable to us in that it does not designate how exclusiveness is achieved and therefore includes both defensive and avoidance behavior with respect to space. According to Brown and Orians (1970: 242) "the acts recognized as defense of an area include two categories, namely: (1) actual defense, such as attacking, chasing, and threatening rival intruders, and (2) identifying acts that designate the defender and make his presence conspicuous to rivals." Avoidance behavior is less clearly definable and has received less attention than defensive behavior; it presumably derives from previous experience with defensive and/or designatory behavior of the territory owners in specific areas.

A second concept, that of home range, should also be defined. According to Brown and Orians (1970: 240) home range is "the area in which an animal normally lives, exclusive of migrations, emigrations, or unusual erratic wanderings." It is "defined and estimated without reference to the presence or absence of particular types of behavior . . . or of other individuals."

Home Range

For Acorn Woodpeckers at Hastings, home range was generally coterminous with territory. Some groups did not have naturally occurring water on their territories and occasionally left them to obtain it. The members of several groups may use the same water source, and when it is not on any group's territory complete overlap in area used occurs without defensive behavior being shown. As a result of local acorn crop failures, some groups collected nuts outside their territories, but in these circumstances the birds defended the trees from which they harvested nuts from the members of other groups. Strictly speaking such new areas are part of the territory even though there may be undefended areas between the harvest trees and the home area.

INTRASPECIFIC TERRITORY

The members of each group jointly defend a year-round, all-purpose territory from conspecifics of other groups. At Hastings the size of the defended area ranged from about 3.5 to 9 ha (average 6). Both males and females defend the territory. Young fledglings begin doing so about 2 months after fledging.

Figure 5 shows the study area and the distribution of territories from 1971 to 1974. Encircled areas indicate approximate territorial boundaries. Boundaries shifted in some cases, and some territories were abandoned for varying periods of time. No group was bounded on all sides by other groups, which made it difficult in some cases to estimate boundaries precisely. But by encompassing all points where defense occurred and taking into account areas avoided by conspecifics of neighboring groups, it was possible to obtain a fair estimate of territory size.

At Hastings intraspecific territorial encounters occurred most frequently in March–April and August–September. These periods coincide with movements of birds in the late summer associated with food failure on the home territory and movements in the spring associated with recolonizing of territories abandoned the previous autumn or winter. Also in the spring individuals may change groups.

Some quantified information on intraspecific territorial defense is given in a previous paper (MacRoberts 1970). In this section we will be concerned primarily with the behavior of intruding and defending birds.

Intruding conspecifics are behaviorally easily distinguished from residents. An intruder of course flies onto the territory from outside it. Flight paths used by intruders usually differ from those used by residents. They land at places where residents (rarely) perch, generally in the tops of trees peripheral to the center of the territory. Intruders often assume a sleeked appearance with feathers flattened and necks elongated and tend to look around much more than residents. Additionally they do not approach residents. How residents recognize intruders is not always obvious, but they are usually quick to discover their presence and often recognize them before they land in the territory. Sometimes a resident flies toward an intruder before it lands and may even intercept it in flight. Obviously recognition in these cases is visual.

Conspecific intruders may (1) leave immediately of their own accord, (2) be chased from the territory by one or more residents, (3) remain on another group's territory for hours or even days, (4) join the resident group, or (5) take over a section or all of the territory and exclude the residents.

Intruders, unless they soon leave of their own accord, are invariably chased. Chasing consists of one or more residents flying at the intruder. The intruder usually flies before the residents reach it. If the intruder is persistent, a series of chases follow: intruder landing, residents flying toward and landing nearby, intruder flying. Continuous aerial chases may occur during which the intruder is pursued without pause. Such pursuits generally involve several residents and may occur in relays; as one resident drops out of the chase, others take up pursuit. If the intruder is caught, the two birds grapple and may fall interlocked to the ground where the struggle continues.

When an intruder attempts to join another group, protracted chasing as described above occurs, but after a few days the frequency of chasing drops and the intruder begins to approach residents and give the *waka* display (see Appendix I for a discussion of displays). Initially the intruder is immediately chased, but slowly the residents begin to respond by *waka* displaying. Later, as an accepted member of the group, the intruder becomes for a time the individual that most frequently initiates displaying. This same pattern occurs whether a single intruder or several are involved.

We saw one unusual example of intruders joining another group. It involved the entire membership of one group joining a neighboring group. Once the situation was stable, the majority of the intruders returned to their old territory leaving behind two of their members. These two birds frequented both the new area and the old territory for a few days but eventually became permanent members of the neighboring group.

When birds expand their territory or take over the territory of another group, they do not remain submissive—instead of fleeing when approached by residents, they attack. This leads to frequent grappling as birds of neither group tend to flee. Such encounters may result in the entire territory or parts of it changing ownership very rapidly, sometimes in a matter of minutes. It appears that numerical superiority is important as in no case of take-over did we observe a smaller group displace a larger one. In one such territorial encounter, during 2 days one group gradually took over, one by one, several trees on another's territory. One intruder would fly to a tree within the residents' territory and perch there. Residents would fly to the same tree, followed by more intruders, then more residents. Intense chasing, grappling, and displaying immediately followed, and after a few minutes the residents, one by one, returned to parts of the territory not then in dispute. The intruders, now the "owners," remained and chased any of the old residents that entered their areas.

Little interaction normally occurs along boundaries of established groups. When one group takes over part of another's territory however, boundaries become a focal point of activity. Once the take-over is completed, the two groups display on opposite sides of the boundary and engage in *waka* gatherings. Such interactions go on for days with diminishing frequency until the situation stabilizes.

Occasionally in boundary disputes the area is not easily divisible by means of designated points. An example of this occurred with reference to a barn roof, of which one group held the greater part. The two groups frequently assembled on their portions, sat opposite each other only a few meters apart and repeatedly *waka* displayed. Opposing individuals flew at each other and hovering above the "line," pecked each other.

INTERSPECIFIC DEFENSE

The members of each group chase birds and small mammals from their granaries and sap trees, from the oaks where they harvest acorns, from their roosts and nests, and occasionally from anvils and hawking perches. Some of these areas are defended only when the woodpeckers are using them; others are defended year-round.

This aspect of Acorn Woodpecker behavior has been described in a previous paper (MacRoberts 1970) containing some quantified material, most of which will not be repeated here.

Chasing is the usual mode of defense used by the woodpeckers. A single woodpecker flying at an intruder is generally sufficient to chase it away. Occasionally intruders are pursued out of the defended area. This was particularly common at Hastings when Starlings (*Sturnus vulgaris*) attempted to enter roosts and nests and when corvids entered harvest trees or granaries. The woodpeckers also mob intruders that persist in the defended area. Mobbing consists of one or more residents making one or a series of aerial passes at the intruder. Passes are swooping dives that take the defender close to the intruder, which may then be pecked. More rarely the woodpeckers land near or hover above the intruder and peck it. The *karrit-cut* display may be given during mobbing.

The woodpeckers chase all heterospecific birds and small mammals from their storage areas, whether or not the granaries contain stores. Persistent and frequent intruders at Hastings were California Ground Squirrels (*Spermophilus beecheyi*), White-breasted Nuthatches (*Sitta carolinensis*), and corvids. The rate of interaction between the woodpeckers and other species in the storage areas generally did not exceed one or two per hour of observation.

No group at Hastings suffered major depredations. Western Gray Squirrels (*Sciurus griseus*) are not common at Hastings in any locality inhabited by the woodpeckers, and, although California Ground Squirrels made inroads into the stores of some groups, these never resulted in a complete loss of stores.

What can occur is illustrated by the following example. In 1966 we observed a group of five Acorn Woodpeckers near Orinda, California. This group had four large storage trees that they lost to Fox Squirrels (*Sciurus niger*) over a period of about 2 weeks. The rate of encounter between the woodpeckers and other species in the storage areas averaged about 15 per hour, of which half involved squirrels. The squirrels were persistent in their attempts to steal nuts and often remained in the granaries under constant attack. On one occasion, even though five woodpeckers made 73 aerial passes at a single squirrel, it was able to extract an acorn and quit the area (MacRoberts 1970).

In addition to year-round defense of storage sites, the woodpeckers defend the oaks from which they gather acorns. Defense is limited to the period during which the birds eat and store green nuts.

At Hastings interactions involved corvids but also Ground Squirrels, Gray Squirrels, Band-tailed Pigeons (*Columba fasciata*), Common Flickers (*Colaptes auratus*), and White-breasted Nuthatches, among others. During most years at Hastings the nut crop was good, and the rate of conflict between woodpeckers and other species was low. In 1973 however the acorn crop was very patchy in some areas with only some trees producing a good supply of nuts, and the rate of interaction between the woodpeckers and other species in these trees was high. In one area, Scrub Jays and Yellow-billed Magpies were chased from a single Valley Oak about once every 5 min. In this instance the group (four woodpeckers) succeeded in keeping their harvest tree relatively free of intruders; the jays and magpies, rather than attempting to pick acorns directly from the tree, went to the ground for fallen ones. A large flock of Common Crows (*Corvus brachyrhynchos*) located this particular tree and came in such numbers that defense failed. The woodpeckers and crows harvested from the tree, each taking nuts the other probably would have used.

A third resource defended from other species are sap trees. These, like the harvest oaks, are defended only when the woodpeckers are using them. Birds that frequently entered and were chased from sap borings were Plain Titmice (*Parus inornatus*), Nuttall's Woodpeckers (*Dendrocopos nuttallii*), White-breasted Nuthatches, and Anna's Hummingbirds (*Calypte anna*). The only mammals seen to enter sap trees were Merriam's Chipmunks (*Eutamias merriami*), which also were chased out.

In addition to the quantified material available in a previous paper (MacRoberts 1970), we made one series of observations on the effect of the presence or absence of woodpeckers in sap trees on the rate of heterospecific

TABLE 5

RATE OF HETEROSPECIFIC INTRUSION INTO AN ACORN WOODPECKER SAP TREE

	Woodpeckers present (957 min)		Woodpeckers absent (118 min)
	Number of intruders	Number of times chased out	Number of intruders
White-breasted Nuthatch	38	16	25
Anna's Hummingbird	5	4	24
Nuttall's Woodpecker	1	1	3
Plain Titmouse	2	1	2
Total	46	22	54

intrusion (Table 5). The tree was watched daily for a total of 1075 min from 9 to 14 July, and the presence and absence of Acorn Woodpeckers and other species in the tree were noted and timed. During this period the woodpeckers were present in the tree for 957 min and absent for 118 min. Intruders entered the tree 46 times when the woodpeckers were present, and each intruder spent from 1 to 62 sec in it. When the woodpeckers were absent, 54 intruders entered the tree and each spent from 1 to 90 sec there. When the tree was occupied by woodpeckers one intruder entered every 21 min on average; when not occupied by woodpeckers, one intruder entered every 2 min on average. The average duration of intrusion when the tree was occupied by woodpeckers was about 10 sec; when unocccupied, it was about 23 sec. Dividing the time spent by intruders in the tree by the total observation time gives a factor of less than 1% occupancy in the presence of woodpeckers and slightly over 17% when the woodpeckers were absent. When the tree was occupied by woodpeckers, about half of the intruders were chased from it and others left of their own accord. The different rates of intrusion by hummingbirds seem interesting in this regard. They entered the sap tree almost exclusively when the woodpeckers were absent. The relatively long periods of time spent by intruders in the tree when the woodpeckers were present relate to one particular circumstance. The woodpecker group had a single fledgling in 1973. Although this bird was an avid sap eater, it was not an effective defender, and when alone in the sap tree it often allowed intruders to enter. It was only when an older bird was present that the sap tree was kept virtually free of intruders.

These figures show clearly the effect of defense by the woodpeckers and illustrate the effectiveness of similar defense of other areas. Intruders enter such areas much less frequently when woodpeckers are present, presumably having learned to avoid them.

FIGURE 21. An Acorn Woodpecker chasing a Lewis' Woodpecker from an insect hawking perch.

Defense of roosts and nests is characteristic of many hole-nesting birds (von Haartman 1971). Many animals will use the woodpeckers' roosts and, especially during the breeding season, the woodpeckers chase those that approach these areas. In our experience only Starlings, Ash-throated Flycatchers (*Myiarchus cinerascens*), and Violet-green Swallows (*Tachycineta thalassina*) nested in the woodpeckers' cavities. Starlings and Western Bluebirds persistently approached the holes and were always chased off. Starlings are not yet common at Hastings, but in some areas their nesting habits conflict with those of the Acorn Woodpecker (Troetschler 1969).

The woodpeckers defend their hawking perches and, especially, anvils at which acorns and acorn fragments are often left. This results in frequent visits by Plain Titmice, White-breasted Nuthatches, and occasionally Brown Towhees (*Pipilo fuscus*). We also observed the woodpeckers chase California Quail (*Lophortyx californicus*) from oat anvils. Although hawking perches are not often defended and intruders are tolerated even when a woodpecker is flycatching nearby, almost any small bird may be chased from them (Fig. 21).

TABLE 6

DOMINANCE HIERARCHY IN GROUP 2 DURING WINTER OF 1971–72[1]

			Bird dominating						
Bird dominated	Sex	Year fledged	WGB1	WP	Unbanded female	WR	Unbanded male	WDB	WBY
WGB1	♂	?	—						
WP	♂	?	3	—					
Unbanded	♀	?		2	—	10			
WR	♀	?	1	4	7	—			
Unbanded	♂	1971	1	30	10	3	—		
WDB	♂	1971		19	11	4	21	—	1
WBY	♀	1971	1	12	16	8	15	14	—

[1] WGB1 disappeared from group in December 1971. WR and unbanded female reversed rank in mid-January 1972. See text.

INTRAGROUP SPACING

The members of each group can be ranked in a dominance hierarchy. Dominant-subordinate relationships develop soon after fledging. Dominance rank is especially important in certain types of competitive feeding interactions among juveniles. Adult-adult dominance interactions are infrequent and usually occur when individual distance is violated.

The factors determining rank are not entirely clear, but age and sex are important. Males outrank females in each age class and older individuals outrank younger ones. Relative ranks were stable over long periods although there were occasional reversals. Tables 6 and 7 show the dominance relations in one group over the period 1971 to 1974. The behaviors used in compiling these tables were pecking another individual and chatter calling, hunching, and facing away in the presence of another group member.

Under most conditions Acorn Woodpeckers classify as a "distance" species (Conder 1949). Individuals generally do not make physical contact but

TABLE 7

DOMINANCE HIERARCHY IN GROUP 2 FROM SUMMER 1972 TO SPRING 1974

			Bird dominating			
Bird dominated	Sex	Year fledged	WP	Unbanded female	WBY	RDG
WP	♂	?	—			
Unbanded	♀	?	2	—		
WBY	♀	1971	7	2	—	
RDG	♀	1972	12	4	17	—

typically keep about 15 to 30 cm from other group members. Unlike many social living species, Acorn Woodpeckers do not mutually preen.

Distance is maintained either by moving away when approached too closely or by not approaching others any nearer than the prescribed distance. When two individuals are in close proximity, the subordinate usually moves away. When distance is violated, one bird may attack the other. This occurs most frequently when juveniles are begging food from older birds.

Situations in which individual distance is not maintained include roosting communally (with as many as 12 birds sharing a cavity), mounting, during *waka* displays, and when juveniles beg food.

In some groups adults defend granaries from first-year birds. Defense begins with acorn storage in late summer or early autumn and may continue through the winter. We will describe this type of defense for the one group that we knew best. The group consisted of eight birds in the autumn of 1971, four of which were in their first year. Although only a part of the main granary, a large Valley Oak, was used for storage, the immature birds were excluded from the entire tree and from the inside of a barn that also served as a granary. Any young bird that entered these areas was attacked and chased out. Otherwise they had free run of the territory, which included a granary of secondary importance.

The acorns in the secondary granary were exhausted by 25 November. Nevertheless the youngsters continued to feed almost exclusively on acorns that were either brought to the secondary granary by the adults or that they recovered themselves from the barn rafters and roof by pecking through the redwood shakes from the outside. They also obtained acorns by invading the main granaries after the adults had gone to roost at dusk.

By mid-December three adults and three juveniles remained in the group. At this time the adults began to allow a first-year female into the main granary but continued to exclude the two immature males. In a period of 3 days the severity of attacks on this bird lessened until she was allowed complete access to the main granary. She did not force her way into the granary but was "allowed" into it. In February the group began eating sap from an area in the main granary, and at this time the immature males were allowed into the tree to sapsuck but were still excluded from stored acorns. In the spring they began spending most of their time away from the group and in April they finally moved about a kilometer away.

In the following year this group, now with one adult male and two adult females, had two young, one of which disappeared shortly after fledging. The surviving youngster was allowed into all granaries.

In other groups with young the same pattern was observed. In some, young were kept out of granaries for a variable period of time and in others they were allowed access to the stores. The factors involved in whether or not young are excluded are not clear, but the decision appears to depend in part on the number of young present in the group. Groups with only one juvenile appear to allow it into granaries; groups with several young deny them such access. In all cases however only young of the year were excluded.

In most groups little or no competition exists among adults for food. The consequences of depletion of food sources and acorn crop failure are discussed in the section on population dynamics. What interests us here is that when food does run short, individuals do not usually defend what remains in the granaries from other group members. All continue to use the stores until these are exhausted. In one case however, the food supply was artificially manipulated. Group 2 in the spring of 1973 had nearly depleted their acorn stores. In order to note the effect of a large supply of food artificially introduced to this group, we put a piece of storage limb containing about 100 acorns in the main granary. The woodpeckers immediately began using these stores and re-stored the majority in their own storage holes, but the most dominant individual began defending the limb from the other birds. He attacked any individual that landed on it, and the other birds began to avoid it when he was there. In his absence the second ranking individual occupied the limb and prevented the two subordinate birds from taking acorns. Such interactions among group members over stored acorns were not seen in any other context.

DISCUSSION OF SPACING

With regard to intraspecific territory three points are clear: (1) in most years the area defended provides all of a group's necessities, that is it is a year-round, all-purpose territory; (2) no overlap of territories occurs between neighboring groups; and (3) the area defended is larger than the area in use at any one period of time. In one year the woodpeckers may use only a portion of the territory extensively, and in the following year different areas may become important because of variations in acorn production, insect abundance, and other factors. Areas not in use are defended and may become important later—certainly the strategy involved is clear.

Group size is probably important in the effectiveness of intra- and interspecific defense. A smaller group never displaced a larger group from their territory although the reverse occurred several times, both in terms of complete take-over and boundary expansion. We did not collect quantified information on group size as this relates to effectiveness of interspecific defense, but it seems probable that defense would be facilitated by large numbers of individuals both in terms of detection and deterence of intruders. In this regard large groups would have an advantage over small groups.

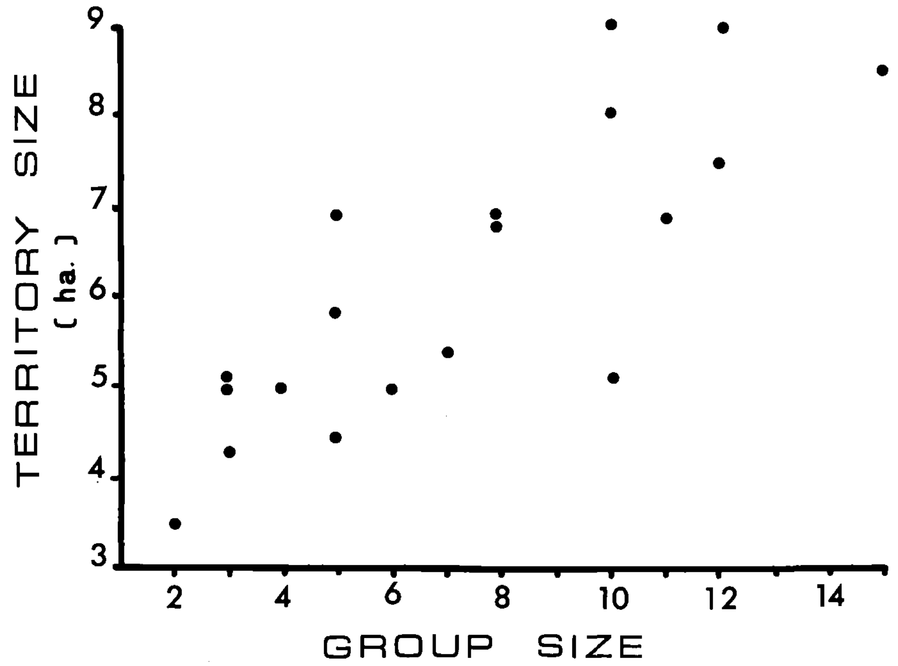


FIGURE 22. Relationship between territory size and maximum group size. See text for further explanation.

Among Acorn Woodpecker groups at Hastings a significant rank correlation existed between group size and territory size (Fig. 22) ($r_s = 0.87$, $P < 0.01$). Although territory size is correlated with group size, it is not proportional to it. Small groups have disproportionately large territories.

The correlation indicates that as a group grows it expands its territory. However, the reverse does not always occur. Reduction in group size was not followed by a reduction in defended area for any of the groups at Hastings. We observed several instances of groups expanding their territories at the expense of other groups, but in all instances expansion involved large groups taking land from small groups. It seems plausible therefore that as a group grows it may expand its holding at the expense of neighboring groups if they are smaller in size.

Within any particular habitat a minimum territory size necessary to support a group and a maximum size that can be defended probably exists. Most groups in the absence of competition will probably occupy areas approaching the maximum, but under competitive conditions only large groups will occupy maximum areas.

Schoener (1968) found a correlation between avian breeding territory size and body weight: small bird species have smaller territories than larger species with similar dietary requirements. He concludes (op. cit.: 138) "it is difficult to reconcile these trends with any of the [previously] proposed functions [of territory] except those directly concerned with limiting the number of individuals using a food resource in a given area." Schoener's review includes no woodpeckers, presumably because little is known about territoriality in this family. However, a comparison of the size of Acorn Woodpecker territories with Schoener's figures indicates that this species at Hastings maintains territories within the predicted range for similar sized, omnivorous species. Acorn Woodpeckers weigh about 75 g and the average territory is about 6 ha. This suggests that the nutritional requirements of a group are an important variable determining territory size, but as territory size does not increase proportionately to increases in group size, presumably the nutritional requirements of each individual can be satisfactorily met by proportionately smaller increases in territory size.

As Brown and Orians (1970: 251) point out: "there is no reason to expect an exact correlation between food supply and territory size, particularly if there is no clue at the time of territory establishment as to what the level of food will be later." This would be especially true for the Acorn Woodpecker in which a group occupies the same territory for years but one in which the food supply varies markedly from year to year. It was only in situations of total acorn failure or when the crop was very poor that groups moved or expanded their territories. We observed no instance of a group reducing the size of their territory in response to an abundant acorn crop.

The function of interspecific defense was clearly indicated in each case. Most defense is related to foods that are highly localized (e.g. stored acorns and sap trees). The defended area is proportional to the spatial distribution of the food supply being exploited. Only in the case of defense of empty storage trees, roosts, and nests is another explanation necessary. Defense of nests and roosts is understandable considering the potential competition for these sites and the energy required in their construction. Possibly defense of an empty granary is directed at animals that forage by boring for insects and might destroy many storage holes.

The woodpeckers in many cases are defending areas from species that exploit exactly the same resources or that are stealing food from them. They overlap with these species at least temporarily in resource use, and it is by behavioral means that divergence in use is achieved. In years of acorn abundance, for example, corvids (particularly Scrub Jays and Common Crows) and Acorn Woodpeckers did not compete to any extent. Each species harvested nuts from different trees but exploited essentially the same strata. In years of scanty acorn production or when the supply of nuts was very localized, defense of harvest trees from other species resulted in different methods of exploiting the crop; the corvids often went elsewhere or picked nuts up from the ground—a source not used by the woodpeckers—or both corvids and woodpeckers exploited the same source, each taking acorns the other probably would have used. Niche overlap occurred in some cases between the woodpeckers and Scrub Jays because the woodpeckers, being less agile, were unable to defend Coast Live Oak harvest trees from them.

As pointed out by Orians and Willson (1964) and later elaborated by Brown and Orians (1970: 254) "interspecific territoriality should be expected among species similar enough morphologically to make exclusion economically possible, under environmental circumstances that facilitate exclusion, and in environments in which highly restricted modes of possible exploitation prevent divergence in resource utilization sufficient to make interspecific exclusion no longer profitable." The woodpeckers' adaptation is to localize food sources (e.g. sap trees, granaries), and this undoubtedly facilitates defense of these sources. The areas defended are those that would be exploited in similar fashion by other animals.

Finally, as regards intragroup defense of granaries, it is unclear why young birds are excluded. They are initially extremely inept at storing acorns and frequently eat stored nuts during the storing period. They may therefore add little to the supply put away or their activities may result in a smaller number of stores than would otherwise be the case. Yet when juveniles are allowed into the granaries they soon become adept at storing and their presence does not seem to result in any drastic loss of nuts.

ROOSTS AND NESTS

Acorn Woodpeckers roost and nest in holes. The same holes may be used for both purposes. As many as 12 or 15 functional holes may exist within a single territory but most groups have fewer. At Hastings the woodpeckers make these holes in living and dead Valley, Blue, Coast Live, and Black Oaks, California Sycamores, and utility poles. The height of cavities above the ground varies from 5 m to the tops of the tallest sycamores some 20 m above the ground. Cavity entrances seldom face upward. In horizontal branches they are face downward and in vertical branches they face the horizon. Entrances are fairly constant in size and may be almost perfectly round. Width (the distance across the entrance at right angles to the long axis of the limb) varied from 51 to 55 mm ($N = 9$; $\bar{x} = 54$). The modal entrance was 55 mm wide. The height of entrances (the distance across the entrance parallel to the long axis of the limb) was more variable and ranged from 50 to 65 mm ($N = 10$; $\bar{x} = 56$). Modal height was 55 mm.

The inner dimensions of cavities are more difficult to obtain. The inner cavity is almost perfectly cylindrical and does not diminish or increase in size

FIGURE 23. Three Acorn Woodpecker cavities in dead Blue Oak.

with depth below the entrance. Diameters of four measured 13, 13, 10, and 8 cm. The latter two in this sample are probably unusually small; they were made in branches with diameters of 13 and 11 cm respectively. The former two are probably more typical. We were able to obtain only two measurements of cavity depth; both were 43 cm. All of the cavities we measured were in fallen limbs, and depth measurements were impossible to obtain because the break almost invariably occurred somewhere across the midline of the cavity, leaving its lower part in the tree and only the entrance and upper part on the ground.

Roosts and nests often weaken the limbs into which they are excavated. The woodpeckers often make a series of cavities in a single limb, one above the other (Fig. 23). If the proximal one breaks, the entire lot falls. In this regard Beatty's (1933) observations are of interest; he found three dead Acorn Woodpeckers in a cavity that had fallen.

Groups roost communally and may use two or more holes simultaneously, with several individuals roosting in each hole or some birds roosting alone. The largest number of individuals we observed roosting together was 12 (the entire membership of the group). It appears that in large groups most birds roost in one hole and the rest in another, but that in small groups all the birds typically roost together. Communal roosting has been noted in other parts of the species' range (Ritter 1938).

The woodpeckers often respond to alarm calls or to the presence of hawks by flying to a roost to hide. In rainy weather the birds spend considerable time inside roosts although more typically they hitch to the undersides of branches.

The woodpeckers lay their eggs and raise young in these cavities. Nests are always in holes in vertical trunks, and cavities that do not have bottoms or tops, that is those in which the entrance leads into a hollow trunk, are never used as nests.

Unfortunately we were unable to obtain much information on the excavation of nests and roosts because the birds spent little time making them. Hole excavation appears to occur primarily in winter and spring. The following observations of one group's work on existing holes may give some indication of the cooperative nature of this activity. The group consisted of six birds, three of which were less than a year old. The adults worked on the roost 59 times, dividing the effort about equally, and the immatures worked on it nine times, each about equally. Frequently the bird working at the hole was relieved by another individual. Forty of these sessions were timed. The longest was 15 min and the shortest only a few seconds, with an average of about 7 min.

It is probable that communal construction of nests and roosts is the rule among these birds and that the older individuals participate most actively. Michael (1929) records a case in which three Acorn Woodpeckers (two males and one female) constructed a nest. Leach (1925,1927), although unable to determine the exact composition of the group he watched, concluded that the members "jointly" built the nest.

REPRODUCTION

The Acorn Woodpecker breeds cooperatively. This habit has been noted at several places in California (Myers 1915, Leach 1925, Michael 1927, Ritter 1938), in Mexico (Martin et al. 1954), and in Central America (Skutch 1969).

In the present study our primary concern was to answer three questions about the breeding system of the Acorn Woodpecker. (1) Which group members are parents? (2) Which group members incubate the eggs, and brood and feed the nestlings and fledglings? (3) What is the fate of fledged young? We have been able to answer only the latter two questions satisfactorily.

We will first present some data collected in relation to the second question and defer questions one and three until later. Question three is dealt with in part in the section on population dynamics.

At Hastings Acorn Woodpeckers begin laying during April and May and young are fledged in late May, June, and early July. The duration of incubation is not known precisely as we did not examine nests for eggs, but it appears to be about 14 to 16 days. The period from hatching to fledging is approximately 30 to 32 days.

1972 Breeding Season

Appendix II gives the composition of the six Hastings groups that were banded and censused by the spring of 1972. These were groups 2, 4, 6, 7, 8, and 15. Only groups 2 and 15 bred in 1972. If any other nests were begun, they were soon lost. Table 8 shows the contribution made by the members of each group for nests watched in 1972 and 1973.

Observations on group 2's nest began on 1 May approximately 10 days before the eggs hatched and continued until about 26 days after the eggs hatched. The nest was watched for about 104 h. Two young fledged.

Observations on group 15's nest began on 2 May about 13 days before the eggs hatched and continued until 8 days after hatching. The nest was watched for 63 h. Four young were fledged.

As only two of the six groups observed in 1972 nested, we made additional observations on four other groups with nests that year. These were groups 9, 12, 14, and 24; none contained banded individuals at the time. All except group 9 contained more than a pair, and in these it was clear that more than a pair were involved in incubation and in brooding and feeding the young.

TABLE 8

NESTING DATA FOR HASTINGS GROUPS IN 1972 AND 1973[1]

Group, bird, sex, and age			Eggs		Nestlings		
			Total number of times in nest	Percent of total time in nest	Total number of times in nest or fed nestlings at nest entrance	Percent of total time in nest	Percent of total feedings
Group 2, 1972							
WP	♂	2+	40	55	148	24	49
Unbanded	♀	2+	17	24	119	3	39
WBY	♀	1	0	0	36	5	12
Unoccupied			47	21	286	68	
Overlap			0	0	6	nil	
Group 15, 1972							
BW	♀	2+	58	41	33	27	28
PLP	♀	2+	18	5	27	32	23
Unbanded	♂	2+	64	30	29	19	24
Unbanded	♀	2+	40	18	30	26	25
Unoccupied			114	11	80	4	
Overlap			54	5	38	8	
Group 21, 1973							
Unbanded	♂ ♂	2+	41	88	44	77	92
Unbanded	♀ ♀	2+	4	5	4	2	8
PWPW	♂	1	2	2	0	0	0
Unoccupied			29	12	41	22	
Overlap			16	7	5	1	
Group 19, 1973							
ROY	♀	2+	17	35	38	22	29
Unbanded	♂	2+	16	29	27	21	21
Unbanded	♀	2+	8	11	31	25	24
OLBOLB	♀	1	5	11	10	6	8
GYGY	♂	2+	5	5	19	9	15
OYOY	♀	1	1	3	4	3	3
Unoccupied			38	8	82	16	
Overlap			10	2	47	2	
Group 9, 1973 (Nest 1)							
Unbanded	♂	2+	33	17			
Unbanded	♀	2+	57	50			
GWPB1	♂	1	18	9			
Unoccupied			88	27			
Overlap			16	3			
Group 9, 1973 (Nest 2)							
Unbanded	♂	2+	10	14	31	15	29
Unbanded	♀	2+	39	46	65	28	62
GWPB1	♂	1	2	3	9	7	9
Unoccupied			47	37	102	50	
Overlap			1	nil	1	nil	

TABLE 8 (continued)

Group, bird, sex, and age			Eggs		Nestlings		
			Total number of times in nest	Percent of total time in nest	Total number of times in nest or fed nestlings at nest entrance	Percent of total time in nest	Percent of total feedings
Group 23, 1973							
Unbanded	♂	2+	10	47	25	7	13
LBDB	♀	2+	9	41	83	8	45
RBP	♂	2+	1	1	25	5	13
PLBDP	♀	1	1	nil	27	3	15
OBm	♀	2+	0	0	25	5	13
Unoccupied			18	12	180	73	
Overlap			1	1	18	1	
Group 24, 1973							
Unbanded	♂	2+	15	27	129	13	34
Unbanded	♀	2+	11	16	24	2	6
RW	♂	2+	14	33	109	17	29
W	♂	5+	11	11	17	1	4
YOLG	♀	2+	9	23	23	5	6
DBLBOG	♀	2+	4	5	60	7	16
DGR	♀	1	0	0	19	2	5
Unoccupied			25	9	342	58	
Overlap			36	24	39	5	
Group 22, 1973 (Nest 1)							
LGWPB1	♀	1	0	0	3	4	7
Unidentified	♀♀		5	11	0	0	0
YDB	♀	2+	22	25	16	36	39
PWm	♂	2+	17	21	11	25	27
GPGP	♂	2+	8	5	7	10	17
Unbanded	♀	2+	30	36	0	0	0
DGLGLBW	♀	2+	0	0	4	1	10
Unoccupied			63	7	42	24	
Overlap			13	5	1	nil	
Group 22, 1973 (Nest 2)							
YDB	♀	2+	13	61	14	28	53
Unbanded	♀	2+	2	6	1	6	4
PWm	♂	2+	1	10	6	28	23
Unidentified	♀♀		1	5	3	11	12
Unidentified	♂♂		1	11	1	3	4
GPGP	♂	2+	0	0	1	nil	4
Unoccupied			11	14	22	24	
Overlap			4	7	2	nil	

[1] The table lists each bird that aided at the nest by group, sex, and age (2+ means two or more years old, no suffix indicates known age), the total number of times each individual entered the nest prior to the eggs hatching, the total number of times each individual entered the nest and/or fed nestlings at nest entrance, the percent of total observed time each individual spent in the nest before and after the eggs hatched (incubating and brooding respectively), and the percent contribution of each individual to feeding the nestlings. Unoccupied refers to the same type of data, but with the nest unattended; that is, total number of times nest not attended. Nil refers to less than one-half of 1%. Two or more individuals sometimes occupied the nest simultaneously, and this is referred to as overlap. In cases where overlap occurred, the percentage occupancy adds to more than 100 unless the overlap is subtracted from the total. In all except groups 19, 21, 22, and 24, all group members aided. See text for further explanation.

1973 BREEDING SEASON

Between midsummer 1972 and the spring of 1973 we banded birds in additional groups to increase our sample size. Several of these groups bred in 1973.

Group 21 was watched primarily because it contained three banded 1-year-old males fledged in the group and banded as nestlings the previous summer. The other birds, not banded until after the 1973 breeding season, included several adult males and two adult females in the group in May 1973. Observations of the nest began on 1 May. The eggs hatched on 13 May and observations continued until 31 May. The nest was watched for 41 h. One young was fledged. Because it was often possible to distinguish individuals by variations in plumage and behavior, it was clear that most if not all of the adults participated in nesting activities. As the majority of the birds in this group were not banded at this time, adult males and adult females are lumped into inclusive categories in Table 8. Two of the 1-year-old males did not participate in nesting activities.

Observations of group 19's nest began on 26 May about 10 days before the eggs hatched. The nest was watched for 26 h. All group members except one adult male aided in the nesting effort. The nest failed for unknown reasons about 14 days after the eggs hatched.

Group 9 had two nests and lost both. The first nest was watched from 15 April until it failed on or about 1 May at the time the eggs hatched. The second nest was begun immediately and was watched from 10 May until it failed on or about 6 June. Nestlings hatched in the second nest on 22 May. The first nest was watched for 36 h and the second for 24 h.

Group 23's nest was watched for 56 h from 12 May to 20 June; the eggs hatched on 20 May. Two young were fledged.

Group 24 fledged six young on about 13 June. Observations began at this nest on 3 May; the eggs hatched on 11 May. The nest was watched for 56 h. All group members except two adult females participated in nesting activities.

Group 22 lost two nests in 1973. Observations began on the first nest on 3 May about 10 days before the eggs hatched. The nest failed when the nestlings were about 5 days old. This nest was watched for 29 h. The second nest was begun soon after the first was lost. It was watched for 15 h from 7 to 12 June. Young hatched on 10 June. Group 22 was the largest group observed during the breeding season; it contained 12 birds of which at least three were yearlings probably fledged in the group the previous year. Only about half of the membership participated in nesting activities and only one of the yearlings took part.

Group 2's nest was watched for only 7 h over three days (11 to 13 June), when for unknown reasons it failed during the egg stage. All group members incubated but as the data are few this group is not included in Table 8.

1974 BREEDING SEASON

During 1974, 19 groups were observed. Twelve of these bred and 10 fledged young. Seven groups either did not breed or lost nests before we could determine whether or not eggs had been laid. In 1974 we made few observations on nests, and the data collected are excluded from Table 8. Information on the 1974 breeding season can be found in Appendix II.

Eight of the 12 groups that bred in 1974 consisted of more than a pair, and in all eight, more than a pair incubated the eggs and brooded and fed the nestlings.

Group 15c was the only group known to have fledged two sets of young in one year and the only group known to have had two nests simultaneously. The group consisted of one female and three males during the 1974 breeding season. The first nest was begun on or about 10 April and was watched in late April and early May. One nestling fledged on 25 May. The second nest was not discovered until after the young had hatched and after the young of the first had fledged. Three young were fledged from it on 28 June. The two nests must have overlapped for about 12 days. All four adults participated in both nestings, but the juvenile fledged from the first nest did not help with the second.

AGE-SEX CONTRIBUTION TO NESTING

Table 9 compares age-sex contribution to nesting. Not all group members participate in the nesting effort. Between 76 and 82% of birds 2 or more years old do so with a smaller percentage of yearlings. In groups that began a second nest after fledging the first, the young from the first did not help with the second. Adult females incubate more frequently than adult males, but adult males brood and feed nestlings more frequently than adult females. The average duration of incubation bouts is about equal for adult males and adult females, and yearling incubation bouts are somewhat shorter. The length of bouts after the eggs have hatched is about equal for adults and yearlings. We watched two nests on 24 occasions to determine which individuals stay in the nest at night. In all cases a single bird was involved and was the most dominant male in the group.

Comparing observed with expected for age-sex class participation in the nesting effort, it is evident that birds 2 or more years old participate to a greater extent than would be expected and that yearlings participate less than would be expected (Table 9). This is based on the assumption that each individual regardless of age or sex should participate equally. Adult female participation in brooding is below expectation.

TABLE 9

COMPARISON OF AGE-SEX CLASS CONTRIBUTION TO NESTING EFFORT[1]

	Before eggs hatch				After eggs hatch			
	Adult males	Adult females	Yearling males	Yearling females	Adult males	Adult females	Yearling males	Yearling females
Number of birds in sample	22	21	7	6	21	20	6	6
Number of birds that participated at nest	18	16	3	3	17	16	1	6
Percent of age-sex class participating	82	76	43	50	81	80	17	100
Observed number of times in nest	285	343	22	7	621	582	9	99
Expected number of times in nest	258.2	246.4	82.1	70.3	519.4	494.6	148.4	148.4
Observed time in nest (min)	5059	5809	233	102	3656	2062	53	437
Expected time in nest (min)	4403	4201	1400	1199	2460	2342	703	703
Observed percent care by age-sex class (number of times in nest)	43.4	52.2	3.3	1.1	47.4	44.4	0.7	7.6
Observed percent care by age-sex class based on time in nest	45.1	51.9	2.1	0.9	58.9	33.2	0.8	7.0
Expected percent care by age-sex class	39.3	37.5	12.5	10.7	39.6	37.7	11.3	11.3
Average length of incubation bouts by age-sex class (in min)	17.8	17.0	10.6	14.6	5.9	3.5	5.9	4.4

[1] Based on Table 8. Summarizes data from groups 2 and 15 in 1972, and groups 9 (both nests), 19, 21, 22 (first nest only), 23, and 24 in 1973. Table is based on 433 h of observation. See text for further explanation.

PARENTAGE

Observations of behavior at the nest suggest that older, more dominant individuals probably produce the clutch, but whether this involves a pair or several individuals remains unknown. At most nests only a few birds are very active in early incubation, and perhaps it is only these individuals that breed. In groups composed of two adults and a yearling, it is probably the older birds that breed.

Observations of mounting did not help unravel the question of which members in a group breed. Mounting occurs throughout the year, and most mounting does not result in copulation (see Appendix I).

We observed mounting involving tail waggling and cloacal contact only 10 times, but in most instances the participants were not identifiable. On a few occasions we observed one female mounted by two males in quick succession. Elaborate courtship behavior, which might provide clues to breeding, appears to be absent from the Acorn Woodpecker repertoire. Precopulatory behavior is perfunctory. A female approaches a male and while standing about 15 to 30 cm away, she may assume a posture resembling that used in the *waka* display except that the wings are not spread. She stands more or less stationary with the tail slightly raised. The male hops over, mounts, and while mounted simultaneously wing-flaps and tail waggles.

Three literature references to copulation in this species exist (Michael 1927; Michael, and Leach *in* Ritter 1938), and each describes multiple mounting in which single females copulated with two males in quick succession. These observations probably would not have been reported had they involved only a pair. But polyandry is at least suggested by the multiple mountings.

Exceptionally large clutches of 10 to 17 eggs have been found (Peyton 1917, Dawson 1923, Ritter 1938) but these are rare. The usual number is fewer than six (Bent 1939). The largest number of young fledged from a single nest at Hastings was six. Nests were not examined to determine clutch size.

At present it is not possible to delineate the breeding structure of Acorn Woodpecker groups. Groups do not appear to break down into mating pairs as in anis (*Crotophaga* spp.) (Davis 1940, Skutch 1959, Vehrencamp-Bradbury pers. comm.). We have no proof that more than one pair within each group mates to produce the eggs, but further study may show that a promiscuous (polygynous or polyandrous) system is involved.

Year-old birds probably never are parents, and especially when they are members of groups containing older birds. Their participation in the breeding effort is small, and it seems likely that they have not come into full reproductive condition. We observed only one group in which the single male was 1 year old (group 7a). This group did not produce a clutch although they refurbished an old nest during the breeding season. This is not evidence for deferred maturity as this group occupied an area surrounded by groups that did not breed either in the year in question or in the previous year. The following year when the male was 2 years old, he and his mate produced a clutch. Sexual maturity for males in this species is therefore reached at most by 2 years.

REPRODUCTIVE SUCCESS

In the 1972 sample of seven groups of known composition, three groups fledged young. In the 1973 sample of 16 groups of known composition, five fledged young. In the 1974 sample of 18 groups of known composition, 10 fledged young. The seven groups observed in 1972 together numbered 31 adults. With eight young fledged, this averages 0.26 young per adult for the total sample. In 1973 the total sample included 83 adults with 17 young fledged or 0.20 per adult. In 1974 the total sample included 82 adults; 23 young were fledged or about 0.28 per adult. These are very low fledging rates considering that about half of the young disappear during their first year.

During the study, 47 groups (including six not discussed above) were observed to determine breeding success. Young were fledged from 21 nests (one group fledged young from two nests in 1 year), and nine nests were begun but failed to fledge young (two groups each had two nests in 1 year but lost both). Twenty groups apparently did not nest although some of these may have started nests and lost them so quickly that they went undetected.

We observed only one group fledge two broods in one season. Another group (group 23 in 1972) began a second nest after fledging the first, but this nest was lost before the young fledged. In all other groups that successfully fledged young, a second nest was not begun. In those groups in which the first nest was lost, only two immediately re-nested (groups 9 and 22 in 1973). The literature contains references to Acorn Woodpecker groups that had as many as three nests in 1 year (Leach 1925), but it is not stated if young fledged from any of them.

Why many groups did not breed and many lost eggs or nestlings is not known. We observed no nest predation, although on one occasion an unidentified Acorn Woodpecker flew directly to a nest and immediately emerged holding in its bill a nestling, which it dropped from the entrance. The remainder of the observation period was normal but on the next day the nest had been abandoned. Intruders from other groups were seen attempting to enter nests on about 10 other occasions, but we doubt that this accounted for the high nest loss. We have no evidence that nestling starvation occurred. In most instances of nest loss the birds normally attended the nest one day and had abandoned it the following day.

How nesting success relates to food supply is not known. We did not measure insect abundance and attempt to correlate this with nesting success. Additionally it is not clear how nesting success relates to the supply of stored acorns. Occasionally nestlings and young fledglings are fed stored acorn cotyledons. This typically occurred on days when insects were scarce. Yet groups that had no acorn stores bred successfully. It is clear that groups are not prevented from breeding because of a lack of nest sites; each group had several suitable cavities within their territory.

Lack (1968) raises the question of group size as it relates to reproductive success in cooperatively breeding birds. The information on this point is conflicting, although there is some evidence that at least in some species the

TABLE 10

FLEDGING SUCCESS PER YEAR AS A FUNCTION OF GROUP SIZE

Group size	Number of young fledged per group						
	0	1	2	3	4	5	6
2	7	–	5	–	–	–	–
3	5	1	1	1	–	–	–
4	3	1	–	–	2	–	–
5	1	–	1	–	–	–	–
6	1	–	–	–	–	–	–
7	2	–	–	1	–	1	–
9	1	–	–	–	–	–	1
10	2	1	–	2	–	–	–
12	1	–	–	–	–	–	–

number of young raised is correlated with group size. For the Acorn Woodpecker it is not yet possible to determine if such a correlation exists. Table 10 summarizes the results obtained in the study. It suggests that large groups may raise larger numbers of young to fledging than small groups, but the data are too few to support generalizations.

BEHAVIORAL ASPECTS OF NEST ATTENDANCE

Prior to egg-laying the birds in each group begin attending a particular nest site. They frequently fly to the entrance and look in and often several individuals gather outside the entrance. Nest-attending may be accompanied by refurbishing in which the nest is enlarged. This appears to consist mainly of removing wood chips with a minimum of excavating. Refurbishing may go on for several weeks, or, as in the case of one group that did not breed, it may go on for months. The birds do not make a new nest each year but use existing cavities—either the same cavity used the previous year or one that has been used only for roosting.

Birds may spend time in the nest as if incubating, but such sitting differs from normal incubation in that the periods between bouts (the unoccupied periods) are extremely variable and generally involve hours rather than seconds or minutes.

Once the clutch is laid however the birds fall into a regular pattern of attendance, and throughout the incubation period at least one bird is in the nest at all times. Birds may terminate a bout without being relieved, but generally a direct change-over takes place.

Nest relief follows a standard pattern. A bird flies to the entrance and either waits outside or peers in. The incubating bird typically responds by coming to the entrance and looking out, at which point the newcomer may move aside until the occupant squeezes out and flies off. If the incubating bird does not come to the entrance, the newcomer may remain for awhile and then fly away or peer inside and finally enter, making the change-over inside the nest.

Two birds, rarely more, may occupy the nest simultaneously. This seems to occur because the incubating bird does not leave the nest when another member of the group comes to relieve it, although one of the birds may move to the entrance and sit looking out.

The duration of incubation bouts ranges from only a few seconds to about 2 h. Typical bouts range from 10 to 20 min. Adult males and adult females differ little in length of bouts, but yearlings regardless of sex sit for shorter periods.

Acorn Woodpeckers brood the young in a pattern similar to incubation for about the first week, after which periods in the nest gradually shorten until they enter only long enough to transfer food and remove feces. When the young are old enough to look out of the nest entrance, they are fed there and attending birds enter the nest only to remove feces. Nest attendance therefore diminishes through the nestling period.

When an individual arrives with food at a nest occupied by a brooding bird, it typically waits outside until the occupant leaves. If the nest is not vacated, the outside bird either enters and feeds the young or simply swallows the insect and leaves. Yearlings sometimes hinder the normal course of events by blocking the entrance when an adult arrives with food. On a number of such occasions we have seen the older bird feed the yearling, which then fed the nestlings or swallowed the insect and left the nest.

When nestlings are old enough to look out of the nest, they alternate at the entrance; one occupies the entrance until fed and then generally immediately backs down and is replaced by another nestling, which remains at the entrance until fed. After fledging, the young continue to be fed by the older members of the group.

POST-FLEDGING: ADULT-JUVENILE RELATIONS

Adult-juvenile interactions center largely on feeding. It was difficult to obtain quantified information on the relative contribution made by each member of a group to feeding of juveniles as the birds are very mobile in this period. Several generalizations are possible: (1) most adults feed the juveniles, (2) the adults feed them indiscriminately, (3) yearlings feed juveniles less often than do older birds, and (4) juveniles do not feed their sibs.

Young fledge in late May, June, and early July. For most groups foods available at this time are sap and insects. Some groups may still have stored acorns, but juveniles do not appear to feed on or be fed these.

Young are fed insects brought to them by older birds for about 2 weeks after fledging, but they soon begin flycatching and soon locate the sap trees.

They spend the majority of the next several weeks in the sap trees, and except for a few insects appear to feed on nothing but sap. At this time they are relatively independent of older birds.

When the woodpeckers begin eating green acorns in late summer however, the juveniles cease feeding on sap and turn their attention to this food. They beg food from older birds and are again dependent on them.

Juveniles are very inept at handling acorns, and it requires about 6 weeks for them to become proficient at picking, carrying, and opening them. By the time groups are well into storing in early or mid-autumn, young birds generally can feed themselves. But if they are excluded from granaries, a dependence relationship develops once again.

Juveniles use several means to obtain acorns from adults. The first involves a direct transfer of food from adult to young. A juvenile simply approaches an older bird that is eating an acorn and begs. As the adult feeds, it feeds the juvenile. Initially juveniles find it difficult to anticipate when the adult intends to feed them, and each time the adult lifts its head to look around or to swallow, they may lean forward to be fed. However, the young eventually distinguish when they are to be fed and when not and act appropriately. The only clues appear to be the presence of food in the adult's bill and a slight intention movement by the adult toward them. Juveniles that approach too closely or try to grab acorns are pecked until they move away. Direct feeding continues with decreasing frequency for about 6 weeks, but individuals as old as 10 months occasionally are fed in this manner.

When the older birds first begin feeding on green acorns the young often follow them to and from the harvest trees, but as the season progresses they spend a large proportion of their time at anvils waiting for the adults to arrive with acorns. It is during this period that the juvenile dominance hierarchy becomes most evident. A dominant juvenile attacks subordinates and takes over the best positions next to adults with food. Although an adult may feed two young simultaneously, this is rare and occurs only when the youngsters are on either side of it. What is of interest here is that juveniles are quick to establish a dominance hierarchy among themselves and that the hierarchy appears to be related solely to feeding in terms of priority to adults with food.

A second means used by juveniles to obtain acorns is to scavenge anvils for scraps.

A third method, which develops gradually, is the "rush-and-grab" technique. While begging, a juvenile slowly inches its way close to an adult, grabs the acorn, and quickly turns its back. This technique meets with varying degrees of success, but it is developed by some juveniles to a fine art!

A fourth technique, "crowding-out," is used with particular success at anvils that tend toward the vertical. While begging, a juvenile slowly hitches backward toward a feeding adult until first its tail and then its body is over the acorn, blocking the adult's access to the nut. The juvenile then appropriates the acorn.

A fifth method, which is used by older juveniles, is to sit quietly near an adult working an acorn and appropriate whatever remains when the adult leaves.

Finally, juveniles take acorns from subordinate sibs. Competitive interactions over acorns are common among juveniles, but they seldom occur among adults.

In groups in which young are excluded from granaries they continue to be fed by older birds. They spend the majority of their time during the winter in trees close to the granaries, and the adults bring acorns to them. They are seldom fed directly although they may take acorns by rush-and-grab or crowding-out techniques. Typically the older birds simply leave the acorns or eat part and store the remainder in these trees. Stores are soon appropriated by the youngsters. This "provisioning" continues until the adults allow the young into the main granaries.

Begging may continue into a bird's second year, although this appears to be rare. We observed it in one group that depleted its acorn stores in March-April. A bird 20 months old and one 10 months old began begging from older birds apparently in response to the dwindling food supply.

Juveniles are not at first adept at storing acorns, and when they are excluded from the granaries many juveniles get little practice in storing until their second year. The following example gives an impression of a juvenile's first attempts at storing: RDG flies from the harvest tree to the utility pole carrying an acorn that still has its cap. She hops around there for a few seconds with the acorn in her bill, then flies to the main storage tree where she puts it in one knot hole, then into another. She carries it about, now with the cap end foremost, now reversed, putting it on anvils, in large holes, and other such places. She finally leaves it in a large crack with the cap still attached. She then flies to another knothole and retrieves a nut from it that she must have left there earlier. She carries it about but later returns it to the hole.

Nine days later we observed the same bird: RDG has much improved in her storing. She carries the nuts properly and decaps them. She puts the nuts in storage holes correctly but is clumsy at inserting them and pounding them down. She has dropped several acorns while attempting to store them. She still puts some nuts in large knotholes as before, but puts the majority in storage holes.

POPULATION DYNAMICS

In this section we are concerned with some aspects of population dynamics: mortality, immigration, emigration, natality, age structure of groups, and group size.

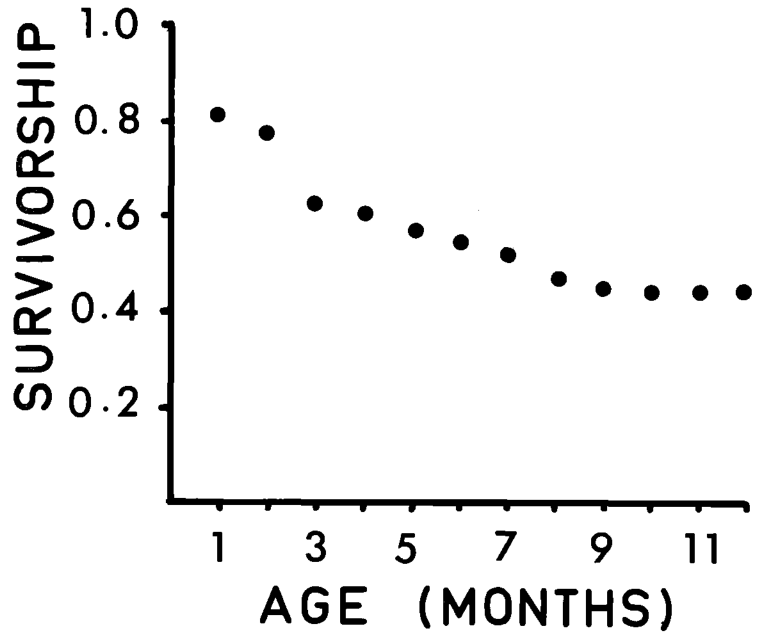


FIGURE 24. Survivorship curve for juvenile Acorn Woodpeckers. Sample consists of 35 individuals banded as nestlings.

About 50 to 60 groups live within the study area (11 km^2). Their distribution is shown in Figure 5 and in the figures contained in this section. Although the number and distribution of groups remained essentially the same throughout the study, the number of individuals constituting the groups changed in most cases (see Appendix II).

MORTALITY

We have little information on starvation. Groups sometimes abandoned their territories and moved, probably either because of acorn crop failure or because of depletion of acorn stores in winter, indicating that food was in short supply. We have no evidence that any individual starved in these circumstances.

Many groups lost eggs and young from nests, but in most cases the causes of such losses were not determined. At least one nestling was killed by another Acorn Woodpecker (see section on Reproductive success, page 56). Nocturnal arboreal mammals may take eggs and nestlings but evidence of this is lacking. On one occasion a Gopher Snake (*Pituophis melanoleucus*) was seen in an Acorn Woodpecker nest tree where it was mobbed by the adults.

Predation is probably high on juveniles especially during the first few months after fledging. Figure 24 gives the survivorship curve for 35 individuals banded as nestlings. Between 50 and 60% of birds banded as nestlings disappeared from the study area during their first year. As some of these birds belonged to groups that left the area and their fates could not be determined, the survivorship curve reflects only minimum survival. As no juvenile is known to have left its group before its first spring, it is assumed that all juveniles disappearing from groups prior to this died, presumably from predation. It is doubtful that starvation is a major cause of death in the summer and early autumn when most juveniles disappear.

Because a large number of adults emigrated from the study area, it is not possible to estimate adult annual mortality precisely. It is probable that mortality among adults is between 0.10 and 0.30 per annum. This estimate is based on the low reproductive rate of Acorn Woodpeckers at Hastings, the fact that group-living birds seem to have higher survival rates than closely related nongroup-living species (Brown 1974), and on the number of individuals at Hastings suspected to have died as compared to the number known to have survived or suspected or known to have emigrated.

WOODPECKER-HAWK INTERACTIONS

The woodpeckers react in characteristic ways to diurnal predatory birds. At Hastings, Cooper's and Sharp-shinned Hawks (*Accipiter cooperi* and *A. striatus*) appear to be the woodpeckers' most important predators, but Red-tailed (*Buteo jamaicensis*) and Red-shouldered Hawks (*B. lineatus*) may be important. The American Kestrel (*Falco sparverius*) is resident, and Merlins (*F. columbarius*), Prairie Falcons (*F. mexicanus*), and Peregrine Falcons (*F. peregrinus*) occur sporadically at Hastings (Linsdale 1947). Although several species of owls occur, the frequency of interaction between them and the woodpeckers is not high, at least during the day.

Typically the woodpeckers respond to flying accipiters by giving the alarm call and hiding, either by hitching to the side of a branch opposite the hawk or by entering a roost hole. The woodpeckers often give alarm calls in response to a flying accipiter even when the hawk is a considerable distance away.

We observed many instances of accipiters diving at woodpeckers. The woodpeckers respond by hitching to the side of a branch opposite the hawk, and just before the hawk strikes, they fly upward in a zigzag pattern and continuously give the *karrit-cut* call. We observed one instance of predation by a Cooper's Hawk. The woodpeckers react similarly to flying buteos but only if they are quite near.

Kestrels are treated differently. A kestrel flying directly at a woodpecker may elicit alarm calling and hiding, but none was seen attempting to catch a woodpecker. Kestrels occasionally are chased by the woodpeckers as illustrated by the following field notes:

A kestrel lands in the top of one of the group's storage trees but away from the stores. The woodpeckers fly at it; it flies and they give chase following it for about 50 m before turning back. About 2 min later a kestrel flies to and lands in the same place. No alarm calls or hiding by the woodpeckers. Several fly over and land about 3 m away from the kestrel and hitch toward it. A male hitches to about 1 m of the kestrel keeping a branch between himself and the falcon. He then flies at the kestrel as do some other group members and all chase it, this time uttering the *karrit-cut.*

The only interaction observed between a woodpecker and any other falcon occurred in the summer of 1972 when either a Prairie Falcon or a Peregrine caught a woodpecker that was sitting on some fallen branches scanning for insects. The falcon caught the woodpecker before it moved.

The woodpeckers react differently to stationary hawks and owls. They may mob owls in the classic manner. They approach, sit near them, and give *karrit-cut* displays. The woodpeckers usually hide from an accipiter that is perched in the territory and remain quiet until it leaves. If the hawk remains for a long time, they resume activity but keep a good distance, usually 30 m or more, from it. When it flies they may emit an alarm call and hide. Stationary buteos elicit siimilar responses although the wooodpeckers are not as wary of them. They hide for only a short time and will approach a perching buteo to within 3 m.

When engaged in almost any activity, except when working inside a roost hole or nest cavity or when sunbathing, the woodpeckers pause every few seconds and look around. Such behavior must certainly relate to predator detection.

On the basis of the two instances of predation observed and on the basis of the responses of the woodpeckers to the various hawk species, we believe that predation by hawks is an important cause of mortality. Accipiters are probably the major predators but buteos and owls also take Acorn Woodpeckers (Fitch et al. 1946, Fitch 1947).

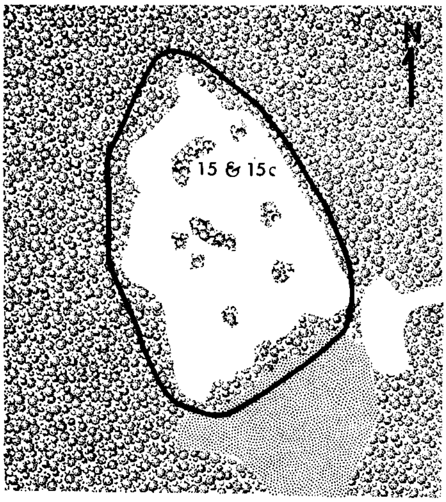
IMMIGRATION AND EMIGRATION

Individuals tend to disperse during two periods of the year: spring and late summer-early autumn. Spring movement usually involves individuals leaving their groups and joining other groups or occupying abandoned territories, but may involve entire groups moving into territories abandoned the previous autumn. Movement in late summer or early autumn almost invariably involves entire groups. It was related directly or indirectly to acorn failure. The circumstances are described below.

TABLE 11
EFFECT OF 1972 ACORN CROP FAILURE ON WOODPECKER GROUPS

Group	Acorn crop	Response of group
2	Acorn failure on only part of territory	Group was able to store enough and remained on territory.
4	Total acorn failure	Moved to School Hill in late summer 1972 and overwintered there. Returned to original territory in spring and summer 1973.
6	Total acorn failure	Moved out of study area in late summer 1972. Not seen again.
7	Total acorn failure	Two members of group moved to School Hill and joined group 12 in late summer 1972. Remainder stayed on territory and gathered nuts from hills outside territory. Abandoned territory in spring 1973 after the two birds that had overwintered on School Hill rejoined group. Fate of group unknown.
8	Total acorn failure	Remained on territory and gathered nuts from hills outside territory. Apparently unable to store enough to survive winter. Abandoned territory in February 1973. Not seen again.
12	Total acorn failure	Moved to School Hill in late summer 1972. Returned to original territory in spring 1973.
13	Total acorn failure	These birds were not banded and their fate is not known. They abandoned their territory in late summer 1972. The territory was reoccupied in spring 1973. Some or all of the reoccupying birds may have been members of group before abandonment.
14	Total acorn failure	Same as group 13.
15	Good acorn crop	Apparently displaced by groups 4, 12, 15a, and 15b in late summer 1972. Fate unknown.
15a	History prior to arrival on School Hill unknown	Moved to School Hill in late summer 1972 but did not store. Moved out of area in November 1972 after acorns had fallen. Fate unknown.
15b	Same as group 15a	Same as group 15a.
16	Same as group 15a	Moved to "ARF" in late summer 1972. Stored in granary that had not been used for several years. Overwintered at "ARF" but abandoned area in spring 1973. One individual moved to group 13. Fate of others unknown.

Although acorn production in the autumn of 1971 was apparently good over most of the reservation, one group, 4, did not lay in many stores. In midwinter its members exhausted their stores and frequented an area about 0.5 km outside their territory where they gathered the few Coast Live Oak



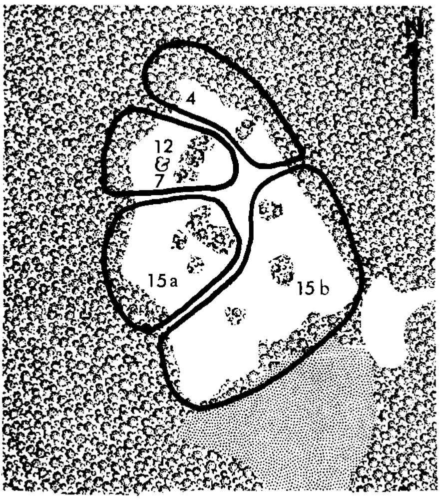


FIGURE 25 (Left). Approximate territorial boundaries for group 15 and 15c. Group 15 occupied the area until late summer 1972. Group 15c occupied the area from summer of 1973 until the study terminated. See text and Appendix II for further information.

FIGURE 26 (Right). Approximate territorial boundaries for groups 4, 7, 12, 15a, and 15b during autumn 1972. Groups 15a and 15b left the area in November. See text and Appendix II.

acorns still remaining on the trees. They moved between their territory and this area daily over a period of weeks, returning to the territory to roost. Two of the five birds that constituted this group disappeared that winter, but whether this related to food scarcity is not known.

In late March 1972, several nights of below freezing temperatures killed the new leaves, flowers, and catkins of all oaks below 550 m elevation. Although the trees later put out new leaves, they did not produce acorns. Table 11 and Figures 25, 26, and 27 in conjunction with Figure 5 summarize the effects of the freeze on the woodpeckers. Most groups within the affected area moved out of the study area in the autumn; others displaced other groups from their territories. During the winter of 1972–73 only groups 2 and 8 and part of group 7 (or about 11 birds) were left in the Big Creek and Finch Creek areas where the previous winter approximately 40 to 50 birds had lived. All territories abandoned were reoccupied in the spring of 1973 but by fewer birds than before.

In 1973 the acorn crop was good in the valleys but generally poor at higher elevations. In some areas no acorns developed, and groups either abandoned their territories and moved or they harvested acorns outside their territories. Table 12 and Figures 28 and 29 summarize the responses of groups.

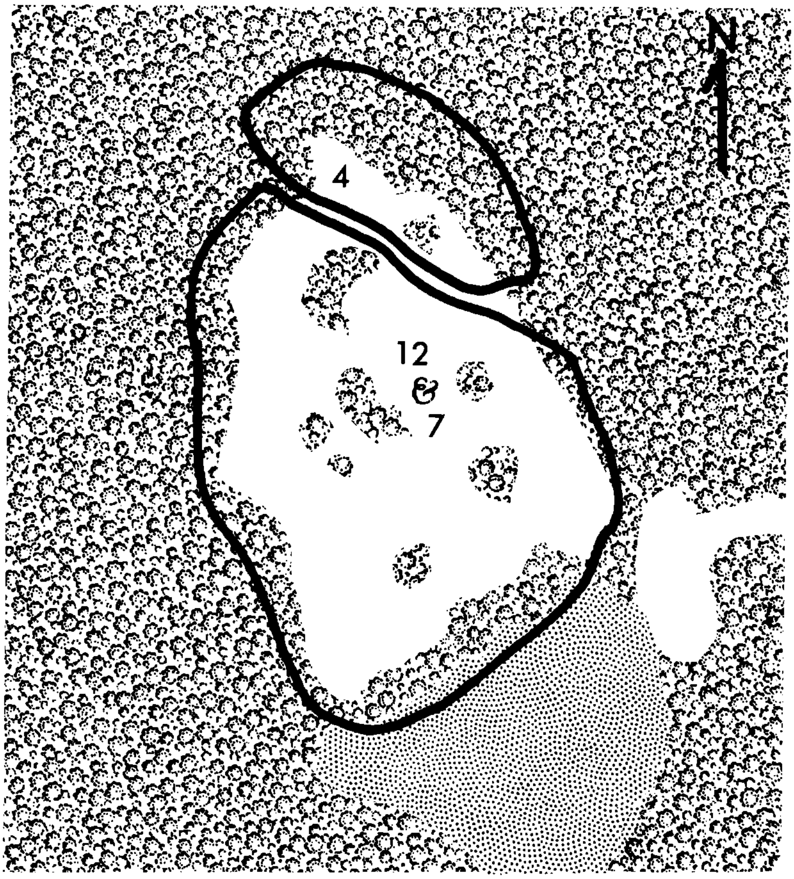


Figure 27. Approximate territorial boundaries for groups 4, 7, and 12 during winter of 1972–73. See text and Appendix II.

The response of group 3 needs further elaboration. Although its members had no acorns on their territory, instead of abandoning it they harvested nuts on group 2's territory and from an area between group 2 and 4 in the valley some 300 m away, and carried them back to their territory. They defended these areas during the autumn of 1973. In spite of the effort of a round trip of 600 m and an elevation change of 100 m, this group (approximately eight birds) stored some 5000 nuts and filled about half of the storage space in their granary.

Beatty (1943) and Michael (1926) recorded similar acorn crop failures in Yosemite Valley, which caused Acorn Woodpeckers to abandon their territories and move out of the valley.

TABLE 12

EFFECT OF 1973 ACORN CROP FAILURE ON WOODPECKER GROUPS

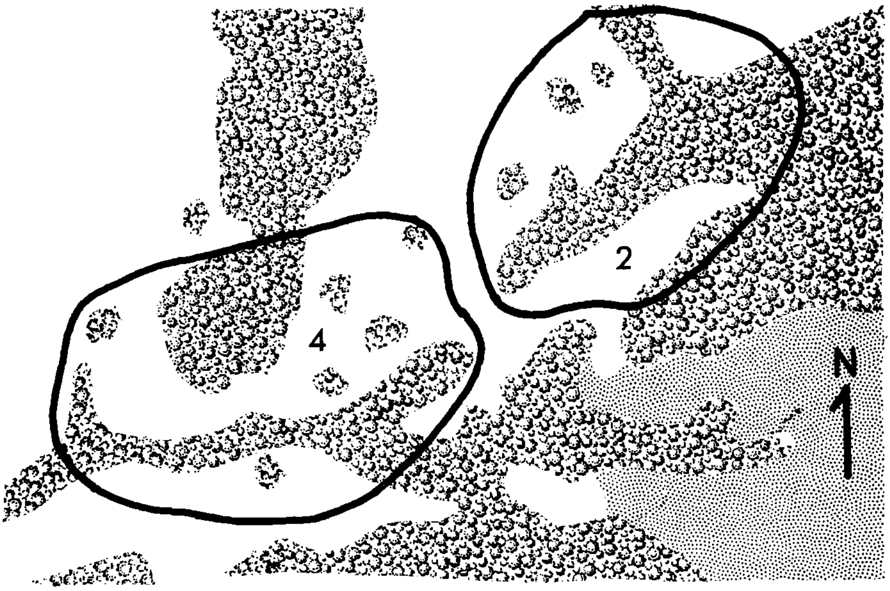
Group	Acorn crop	Response of group
1	Total acorn failure	Moved to area north of groups 2 and 4 in late summer 1973. Stored in Blue Oak without storage holes. Overwintered but returned to original territory in spring 1974.
2	Good acorn crop	Remained on territory, but group 3 invaded eastern part of territory and occupied it from late summer to mid-autumn 1973.
3	Total acorn failure	Displaced group 2 from part of their territory in late summer 1973 and gathered nuts there. Returned to their own territory in mid-autumn after nuts had fallen.
4	Good acorn crop	Remained on territory, but group 5 invaded the western part of territory and occupied it from late summer 1973 to February 1974.
5	Presumably moved because of acorn failure	Occupied part of group 4's territory in late summer 1973. Prior history not known. The birds stored in cracks and under loose bark but ran out of food in February 1974 and abandoned the area at that time. They were not seen again.

In the spring individuals move and occupy empty territories or join other groups. In the study area, territories abandoned in the autumn or winter because of acorn failure were all reoccupied the following spring. The birds that occupied vacated areas were either the original territory holders or were new to the area.

In spring birds may leave their groups and join other groups; cases in point are WR (a female of group 2) and two males from group 24 (see Appendix II). It is also in the spring that first-year birds may leave their natal groups and move into abandoned territories or join other groups.

We observed that individuals may leave their territories and wander. Primarily young birds are involved and usually at two periods of the year: in the late summer and early autumn juveniles fledged that summer may wander, and from early spring to early summer yearlings may do so. Late summer-autumn wandering appears to be related to exclusion of young from granaries; as acorns are available on the trees at this time, the young may go elsewhere to feed. None was observed to leave its group permanently at this time. Such wanderers were seen as far as 2 km from their territories.

While immigration into parts of the study area was high, immigration into existing groups was small. Where territories were abandoned, many were reocccupied by birds that had not lived in them previously, but few outside



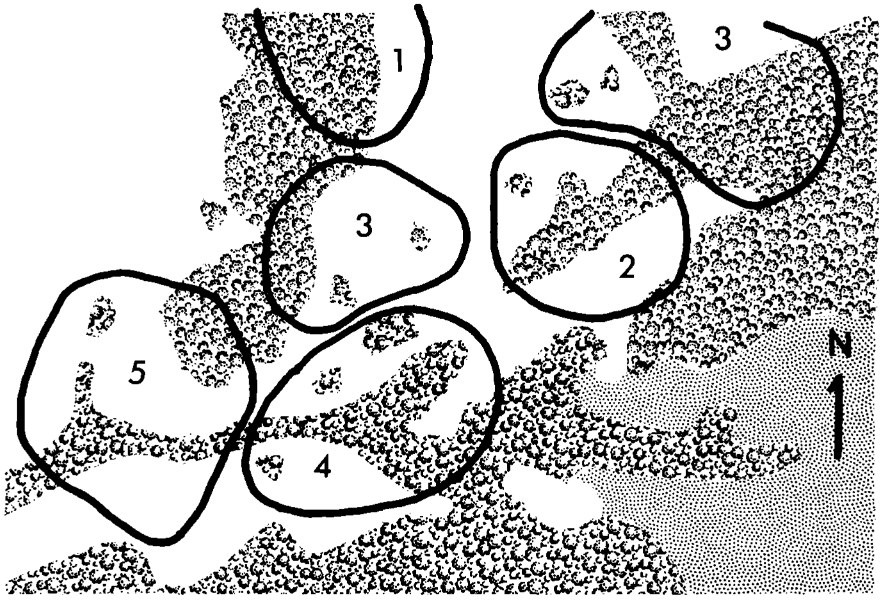


FIGURE 28 (Top). Approximate territorial boundaries for groups 2 and 4 during most of the study. See text and Appendix II.

FIGURE 29 (Bottom). Approximate territorial boundaries for groups 1 to 5 during autumn 1973. Groups 2 and 4 lost parts of their territories to groups 3 and 5. See text and Appendix II for further information.

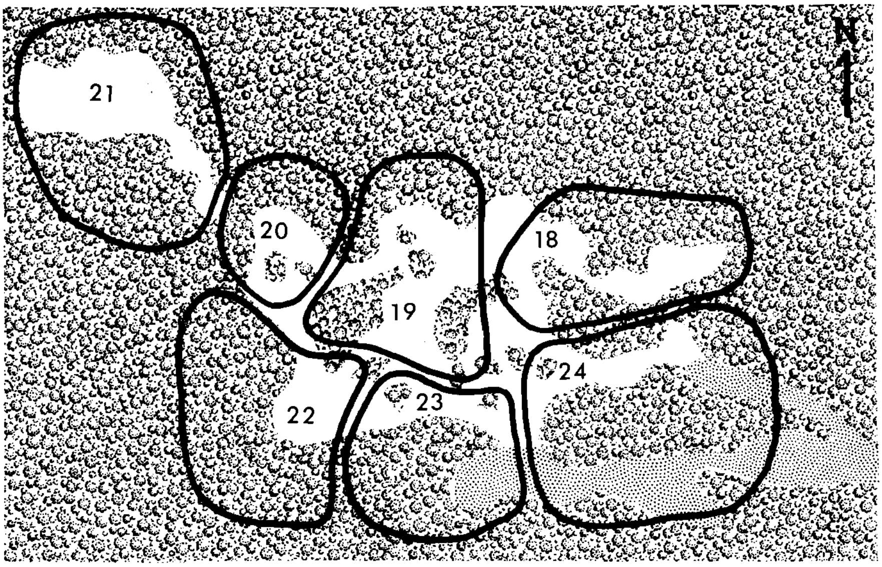


FIGURE 30. Approximate territorial boundaries for groups on the Arnold Field during most of the study. See text and Appendix II.

individuals joined groups that had maintained their territories. Groups that moved often retained their integrity and either took over areas occupied by other groups or lived in areas that previously had not been occupied. Additionally, several individuals of one group sometimes joined another group.

It appears therefore that unless a group is forced out of its territory either by an invading group or because of food failure, its integrity is high and outsiders seldom join. If a group is forced to move, it may lose its integrity.

In addition to those instances described above and in the section on intraspecific territoriality in which one group displaced another, one further example deserves mention. In April 1973, group 22 annexed group 23's sap trees and one of its two storage trees. In July and August of the same year group 22 again expanded at group 23's expense and forced it out of most of the remainder of its territory, including the second storage tree. Through the winter two individuals (one member of group 23 and one unknown bird) remained on the small part of the territory that had not been appropriated. In the summer of 1974 these two birds disappeared. Group 22 then occupied the remainder of the area (Figs. 30 and 31).

Territorial expansion in this case is of interest because it appeared to be unrelated to food. Although group 22's initial move resulted in the appro-

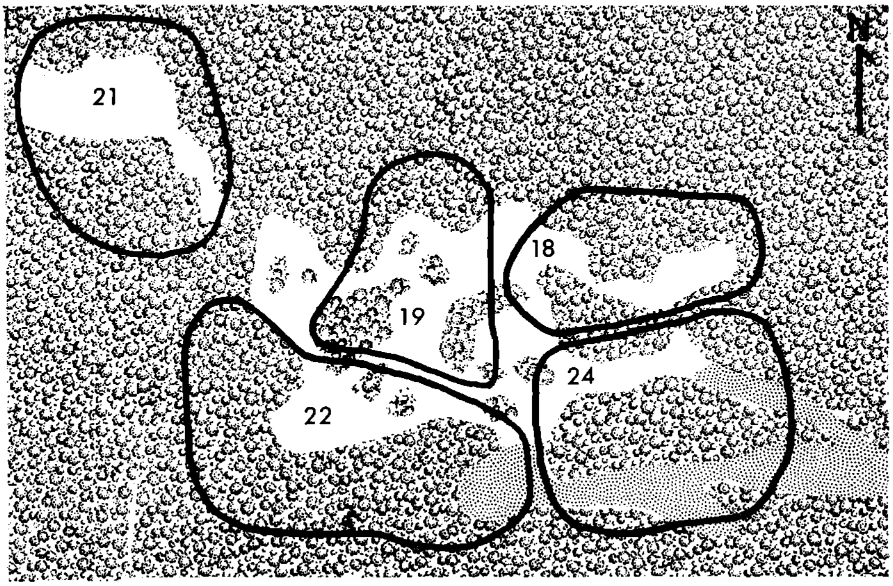


FIGURE 31. Approximate territorial boundaries for groups on the Arnold Field in August 1974. See text and Appendix II.

priation of a granary and sap trees, it did not appear to be stimulated by food shortage at home where both sap and stored acorns were available. Although the circumstances are difficult to interpret, it seems possible that expansion represented an initial stage in one type of group fission. Group 22, with between 12 and 14 individuals, approached the maximum number of birds recorded for any group. A large group may expand at a neighboring group's expense and then divide. Additionally, by midsummer 1973, group 22 occupied a very large territory that was difficult to defend: granaries, sap trees, roosts, and nests were widely scattered and not visible from any one location. Yet no sign that the group was dividing was evident when the study terminated.

RECRUITMENT TO GROUPS

In the study area, the number of young fledged per group was not high. Only about half of the groups fledged young and the average number per year was between 0.2 and 0.3, of which about half disappeared (presumably died) during their first year. All surviving juveniles remained with their groups at least until the following spring when a minority emigrated.

Immigration into established groups was infrequent. We observed only nine instances involving four groups. Some of these need further discussion. Both males that joined group 18 came from the same group. The two females that joined group 12 during the winter of 1972–73 came from the same group and left group 12 before the breeding season. The two females from group 19 that joined group 21 retained ties with their own group and later rejoined it.

The exact genetic relationship among group members was not known in most cases. Considering the low immigration rate and despite the low fledging rates observed, birth appears to be the most important form of recruitment to groups. It seems to us therefore that groups are composed primarily of individuals that are close relatives.

AGE STRUCTURE

On the basis of the data available we believe that between 1971 and 1974 only about 10 to 20% of the total Hastings population was less than a year old. Although it is not possiible to give precise estimates of mean annual adult mortality or future life expectancy because of emigration and immigration and because of the short duration of the study, mortality is apparently low and life expectancy high after a bird reaches 1 year of age.

GROUP SIZE

The upper limit of group size is probably determined by food supply. We have compared the maximum group size in winter on each territory with the number of storage holes and find a significant correlation between the two ($r_s = 0.735$, $P < 0.01$) (Fig. 32). A territory with many storage holes can support a large number of birds, although at any given time fewer than the carrying capacity may use the area. A territory with a small amount of granary space can never support a large group for any length of time. The upper limit of group size therefore should be determined by winter food supply. This depends on the amount of food stored, which in turn depends on the autumn acorn crop and on the number of storage holes. Groups that stored too few acorns or occupied suboptimal habitat where no granaries existed often consumed their food supply in midwinter and were forced to abandon the area at this inhospitable time.

Yet except for complete or almost complete acorn failure, the woodpeckers can persist in areas where annual acorn production fluctuates widely. For example, J. R. Griffin (pers. comm.) measured acorn production of Valley Oaks in drop traps on one Acorn Woodpecker territory and found that the number of acorns recovered between 1971 and 1973 varied between an average of 1 and 32 per tree. It was clear on the basis of additional unquantified observations that the acorn production on this territory was extremely variable. Yet the territory was occupied continuously, and in each year the

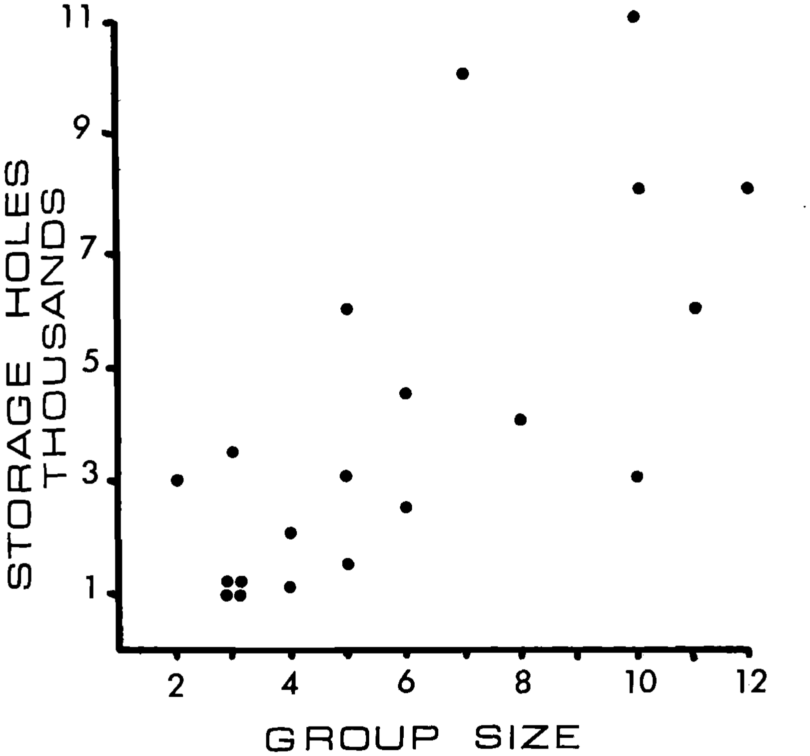


FIGURE 32. Relationship between number of acorn storage holes on each territory and maximum group size. See text for further explanation.

birds stored enough acorns to carry them through the winter. Although in lean years the birds may forage more widely to find nuts, the point remains that even though acorn production may vary markedly from year to year, the woodpeckers appear to be adversely affected only if complete or nearly complete crop failure occurs.

Wynne-Edwards (1962: 322–325) suggested that the Acorn Woodpecker is a species that evolved an "epideictic rite, combining as it does a sampling of the food-supply, a territorial symbol (the [storage] tree), and social competition" that can ultimately lead to the elimination of supernumeraries and determine the reproductive output of the community. An epideictic display is one that functions to give information about numbers in relation to some potentially exhaustible resource, in this case the number of birds in relation to food supply in the form of stored acorns.

Presumably the prediction is that if a group does not have enough stores to support its membership, some individuals will be expelled or will voluntarily leave to prevent "over-fishing" and thereby sacrifice themselves for the benefit of the group. It should follow that groups with excess stores should accept such vagrant individuals. It must also be assumed that after an assessment has been made, groups should not run short of stored nuts.

Wynne-Edwards' group selection hypothesis has been critically examined elsewhere (Hamilton 1964, Lack 1966, Williams 1966). We would like to comment on the suitability of using the Acorn Woodpecker as evidence in favor of this controversial hypothesis. It will be sufficient to summarize our findings as they relate to Wynne-Edwards' discussion of this species. (1) The behaviors described by Ritter and Henshaw that Wynne-Edwards uses as evidence for an "epideictic display" are not associated in any specific way with acorns, granaries, or acorn storing. These behaviors clearly have other functions and most of them are not displays at all. (2) No evidence exists that granaries are "conventional prizes" or that acorn storage has a "ceremonial" function. No evidence exists that acorn storage is anything more than a method by which this species stores food during periods of abundance for use during periods of scarcity (see Lack 1968). (3) Groups do run out of stored nuts, which is not predicted by the hypothesis. (4) The prediction that some birds should leave their groups after storage is completed if not enough food is available to support all individuals is not supported by observation. (5) The hypothesis implies that groups with excess stores should readily accept immigrants, but this does not occur.

The question of how group size is regulated will not be resolved here. The correlation found between group size and amount of granary space indicates that regulation occurs but not how it is actually effected. Unfortunately we have very few observations that bear directly on this matter except those pertaining to groups faced with total acorn failure or depletion of stores in midwinter. Group size is probably regulated by emigration involving younger and/or subordinate members or, as suggested in the example of group 22, it may involve territorial expansion and fissioning of the group. In the few examples of emigration observed, no individual was obviously chased from its group. But certain types of coercion may contribute to an individual's decision to leave, as in those groups in which birds of the year are excluded from granaries and must depend on other birds for food during the winter. If food were to run short, if the young birds continued to be excluded from stores, and if the adults stopped feeding them, this segment of the group would starve or be forced to find food elsewhere. We do not suggest that defense of granaries from birds of the year is a mechanism evolved to encourage dispersal among a certain age class or that it is a way of insuring that some of the group survive if food runs short. Rather, its effect may encourage dispersal.

ECOLOGY AND EVOLUTION OF WOODPECKER SOCIAL SYSTEMS

Little is known about the social organization of the Acorn Woodpecker over most of its range, but the pattern described here is consistent with most reports, which mention its colonial or gregarious habit. Although group size varies in different localities, solitary individuals and pairs are probably the exception.

A few reports suggest that in some areas other systems may occur in this species. In Guatemala, Baepler (1962) states, "This species was restricted to oak-pine forest from 5300 to 6300 feet. In this habitat the birds were frequently seen in small flocks with the Banded-backed Wren [*Thryothorus zonatus*]." Baepler unfortunately does not elaborate. Edwards and Lea (1955: 44) in Chiapas record, "On August 10 and 11 we saw flocks of more than 50 individuals flying, chasing one another noisily and sidling back and forth on horizontal branches in the pine-oak forest." This is the only statement made concerning behavior and although it sounds as if a territorial encounter was observed, the numbers seem exceptionally large. Swarth (1904: 13) apparently observed season-related movements of Acorn Woodpeckers in the Huachuca Mountains in Arizona. "I saw but two or three during February and the early part of March, about the middle of March they began to arrive in numbers, and by April 1 were most abundant." Dickey and van Rossem (1938: 316) state that in El Salvador, "In November and December the Acorn Woodpeckers were in small groups of from two to six, which were probably family parties .... In early spring ... single birds and pairs were much in evidence, the winter groups had evidently broken up as the breeding season drew near."

Otherwise reports as widely scattered as Colombia and Oregon indicate that Acorn Woodpeckers live in permanent groups similar to those described for the present study (Miller 1963). In those areas of Central and South America where the species does not store or stores only in desiccation cracks and under bark, a different type of social oganization probably exists.

For the purpose of discussion we will follow Skutch's (1943, 1948) classification of social systems. The classification is based on the dispersal of young after fledging. The first category includes those species in which a pair attend the nest and the young disperse soon after fledging. Most North American and European woodpeckers exemplify this system. The second category includes those species in which the young do not disperse but remain with their parents through the winter. Some examples are the Golden-naped Woodpecker (*Melanerpes chrysauchen*), probably other *Melanerpes* species, and some piculets (*Picumnus* spp.) (Skutch 1948, 1969). The final category includes those species in which more than a pair attend the nest and groups occupy year-round territories. Examples are the Red-cockaded Woodpecker

(*Dendrocopos borealis*) (Ligon 1970; Thompson 1971), the Acorn Woodpecker, and perhaps the Yellow-tufted Woodpecker (*Melanerpes cruentatus*) (Skutch 1969, Short 1970).

From the information presently available, it is easy to imagine the steps involved in the evolution of group living in woodpeckers. Although other "paths" to sociality have been suggested for other group-living species (for recent reviews see Skutch 1961, Rowley 1968, Harrison 1969, Brown 1974, Koenig MS), group-living in woodpeckers appears to have evolved by nondispersal of young, and groups are primarily family units.

To elucidate the ecological factors that might have been involved in the evolution of group-living in the Acorn Woodpecker, it is necessary to focus attention on the diversity of spacing patterns among other birds and to take cognizance of the similarities and differences among them (Lack 1968). As Orians (1971: 530, following Brown 1964) has pointed out, "once attention was directed toward selection for individual behavior related to space, then many features of the diversity of avian spacing patterns become intelligible with reference to only a few factors, the most important of which are potentially exhaustible resources." In recent years it has become apparent that types of food and their distribution as well as the abundance of suitable nesting sites are strongly correlated with the distribution of the species exploiting them (Crook 1964, Lack 1968, Schoener 1968, von Haartman 1971). The problem then becomes one of explaining the dispersion and dispersal patterns of Acorn Woodpeckers, and this can be done most effectively by comparing them with other similar group-living species, especially those in which sociality involves nondispersal of young.

The Acorn Woodpecker appears to be a species that is living at what Brown (1969) has called level 2 and level 3 population densities. Level 3 refers to population densities sufficiently high so that competition for space prevents some individuals from settling in any but completely unfavorable habitat. A "surplus" of individuals exists. The upper limit of settling density is imposed by the behavior of territorial owners and availability of suitable habitat. When suitable habitat becomes available, the surplus moves into it. Level 2 densities refer to situations in which numbers are sufficiently high so that territorial behavior forces some individuals to settle in suboptimal habitat, which is not crowded but where relative fitness is lowered.

Evidence for level 3 densities includes (1) individuals being prevented from establishing territories in areas already occupied through the aggressive behavior of the residents, (2) ecological evidence of stability of populations, and (3) the existence of a segment of the population capable of breeding but not settled because of no available habitat. Evidence for level 2 densities includes (1) a stable population in some (optimal) habitats and a more fluctuating population in some (suboptimal), (2) individuals prevented from settling in optimal habitat by territorial behavior of residents, and (3) individuals moving from suboptimal to optimal habitat when it is available.

For Acorn Woodpeckers suitable habitat appears to be in short supply. Within the study area territories that were occupied when the study began were still occupied when the study terminated, and no new permanent territories were established. This indicates that all suitable habitat was occupied.

In the spring and summer, the number of groups and their distribution was almost identical each year. In autumn and winter the number of groups changed slightly. These changes were clearly related in all cases to food failure in the autumn, at which time groups without acorns abandoned their territories and moved from the area, displaced other groups, or occupied suboptimal habitat. Areas vacated remained empty until the following spring when all were reoccupied, either by the group that had lived there previously or by birds from other groups. Therefore the summer population, when measured by the number of groups present, and the winter population, when no acorn failure occurred the previous autumn, show practically no variation. Territories following recolonization were identically occupied, that is territorial boundaries were the same even when the colonizing birds had had no previous experience with the area. This suggests that habitat selection by the Acorn Woodpecker is very specific and that some aspect of previously occupied areas increases their suitability over areas that appear suitable but which have not been occupied before. This is of course the presence of granaries, sap trees, roosts, and nests—all modifications of the habitat that are essential, at least in the long run. That all modified habitat is persistently occupied while unmodified habitat is seldom if ever occupied points strongly to the conclusion that all suitable space is occupied, and that when groups are living outside these areas, such areas are in short supply.

The Acorn Woodpecker at Hastings therefore appears to be living at level 3 densities. But there is no "floating" population in the traditional sense of that term. Instead the "surplus" is absorbed by the groups. Young birds did not leave their groups before their first spring and most did not leave then. Dispersion appeared to be prevented by lack of suitable habitat and by the aggressive behavior of territory holders. Although individuals occasionally changed groups, the indications are that the majority that leave their groups occupy areas vacated by other groups. When territories become available they are quickly filled.

The effect of level 3 population density on breeding is not obvious. There appeared to be a large segment of the population that was reproductively mature (2 or more years old, including females) but that probably did not breed. Although the data necessary to demonstrate this point are not presently available, the indications are that within each group only the most dominant individuals breed (whether or not a monogamous system is involved) and that subordinates of either sex, even if they are reproductively mature, do not.

Although autumn movements almost always involved entire groups moving because of acorn crop failure on the home territory, spring movements seldom involved entire groups except when a group reoccupied its old territory. In the spring individuals, either alone or in company of other group members, left their groups and moved to unoccupied territories or forced their way into established groups. The significant aspect of spring movements for the present discussion is that under most conditions this was the only time of year when suitable unoccupied habitat was available. Territories that had been abandoned became suitable only in the spring when insects, sap, and catkins were available. It was at this time that they were reoccupied. It is only in the spring therefore that individuals that would probably be excluded from breeding at home (the low-ranking and younger birds) have the opportunity to disperse and possibly breed, leaving the older, more dominant individuals, which would probably breed in any case, on the home territory. This indicates that except in spring and usually even then, all suitable habitat is occupied. When vacancies are not available, individuals apparently are forced to remain at home.

In the autumn, if a failure in the acorn crop occurs, groups may be forced to settle in suboptimal habitat, that is in areas without granaries, sap trees, roosts, and nests. Examples of this were groups 1, 5, 15a, 15b, 16, and 23 (see Appendix II). Some of these groups managed to store enough acorns in desiccation cracks and under loose bark to survive the winter. Others did not store at all and abandoned these areas in late autumn after all acorns had fallen, and others stored but depleted their stores in winter and quit the area. These groups were undoubtedly prevented from settling in optimal habitat by the territorial behavior of residents. All such winter territories were abandoned in the spring and the groups either returned to their original territories or moved elsewhere.

We may conclude that the woodpeckers are living at level 3 densities most of the time and that periodically level 2 conditions occur in which entire groups move because of food failure and settle temporarily in suboptimal habitat. Mortality among individuals that occupy such areas is probably much greater than among individuals that occupy optimal habitat.

The Acorn Woodpecker occupies habitat in which food supply varies markedly through the year. Insects, sap, acorns, and catkins are seasonal resources, and it is only by storing acorns that food is made available year-round. No naturally occurring food exists in the period between late autumn after the acorns have fallen and early spring when sap, insects, and catkins become available. The behavioral adaptations by which the woodpeckers stabilize a greatly fluctuating but more or less predictable food supply have made them dependent on their own highly specialized modifications of the habitat. Such modified habitat is usually in short supply, but an increased number of individuals can be supported with additional modification.

It appears that sociality in the Acorn Woodpecker has evolved concomitantly with a series of adaptations by the birds in response to a highly fluctuating but annually predictable food supply. Their adaptations to stabilize these fluctuations have created a need for a type of habitat that is highly productive, but which happens to be localized and patchy in distribution. Outside these areas, at least during part of the year, no suitable habitat remains unoccupied. As population pressure increases because young do not disperse, pressure to modify the territory increases. If the basic resources (food, storage trees) are sufficient, the modifications can be carried on (at least in theory) *ad infinitum*. Storage trees with as many as 50,000 holes have been described (Ritter 1938).

The young of many species fare poorly in competition with older birds. Certainly it is easy to imagine the fate of young Acorn Woodpeckers that leave or are forced from their groups in the summer or autumn of their first year. Probably none, unless accompanied by older birds, would be able to force its way into or take over another group's territory and few probably would be able to secure habitat suitable for acorn storage on the scale necessary to carry them through the winter, even if they were as efficient as adults at this task. We know of no juveniles that attempted this, and it is not possible to make comparisons.

Even if the individual could survive alone and in habitat that was not modified, its chances of reproducing probably would not be increased. The bird would either have to attract a mate to its territory—an area that would not be optimal—or it would have to join a group and attempt to breed in it. It would also be extremely vulnerable to invasion by other individuals seeking food and could be easily displaced. As Brown (1969: 316) points out: "The probability of an individual's eventually gaining the opportunity of successful breeding, if the surplus is large and persistent enough, may be greater if it remains within the family group waiting the demise of its elders, . . . than if it forsakes all claims to its old territory and attempts to establish a new one in the face of uniformly fierce defense . . . . Under conditions where the chances of infiltrating another group or establishing a new territory in suitable habitat are remote, an individual can still contribute to raising the frequency of its genes in the population even without actually breeding."

In group-living species an individual's fitness becomes increasingly dependent on others. Each individual, although involved in increasing its relative fitness, must do so by contributing in various ways to the relative fitness of others. Acorn Woodpeckers make such immediate contributions as group defense of territory and helping at the nest. But also each generation depends

TABLE 13

COMPARISONS AMONG LEWIS', RED-HEADED, AND ACORN WOODPECKERS[1]

Characteristic	Lewis'	Red-headed	Acorn
Adult plumage	Monomorphic	Monomorphic	Dimorphic
Juvenile plumage	Distinct	Distinct	Resembles adult male
Distribution:			
breeding	Pairs on pair territory	Pairs on pair territory	Groups on group territories
winter	Individual or pair territories	Individual territories	Groups on group territories
Dispersal	Often moves between breeding and winter grounds, sometimes sedentary	Same as Lewis' Woodpecker	Resident, but with occasional local movement in response to local food failure
Main foods	Mast Insects, caught on wing	Mast Insects caught on wing Maybe sap and bast	Mast Insects caught on wing Sap
Stores acorns	In pieces	Whole and in pieces, seals in stores	Whole and in pieces
Makes storage holes	No	Has been reported but apparently uncommon	Over most of range
Habitat:			
breeding	Savanna, old burns, riparian cottonwoods, oak woodland savanna	Same as Lewis' Woodpecker	Savanna, oak woodland, montane forest where oaks are present; intermediate between Lewis' and Red-headed Woodpeckers' breeding and winter habitats
winter	Oak woodland or vicinity of nut orchards	Same as Lewis' Woodpecker	Same as breeding habitat

[1] Based in part on Bock 1970, Table 18.

on the activities of previous generations; requisite habitat does not occur naturally and granaries, roosts and nests, and sap trees are all modifications that are not easily come by. Each generation adds to the previous generation's labors and in turn probably passes these modifications on to descendants. Such transmission of material wealth should be expected to occur along family lines, and, as is clear, recruitment to groups is mainly by birth. Groups do not readily relinquish their holdings except in dire circumstances.

In its feeding habits the Acorn Woodpecker most closely resembles Lewis' and Red-headed Woodpeckers (Kilham 1963, Skutch 1969, Bock 1970, MacRoberts 1970) but although probably phylogenetically closely related to these species, it has diverged markedly in its social-living habits. Table 13 summarizes some of the similarities and differences among these species. All three store mast, each in a slightly different manner, and all catch insects on the wing.

Although the Lewis' Woodpecker stores whole acorns, it typically stores acorn fragments in desiccation cracks and in other natural crevices; it has not been reported to make storage holes. This species is migratory. It stores in the autumn, subsists on the stores through the winter, and abandons them in the spring when it moves to its breeding grounds. The spring and summer food of Lewis' Woodpeckers is insects caught on the wing.

The Red-headed Woodpecker is also migratory and stores in a manner similar to the Lewis' Woodpecker, but it also has been reported to "enlarge natural cavities or dig pits for separate acorns" (Kilham 1963). Additionally, Red-headed Woodpeckers sometimes seal in winter stores with bits of wood, a behavior that is not found in the other species (Kilham 1958, Skutch 1969, MacRoberts 1975). In the spring however, birds abandon their winter territories and move to breeding grounds where they feed largely on insects. Both the Acorn Woodpecker and the Red-headed Woodpecker eat sap, but how important sap is for the latter is not known.

The habitats of these three species are similar in many respects. In the Acorn Woodpecker elements of both the winter and breeding habitats of the Red-headed and Lewis' Woodpeckers are combined into a single all-purpose, year-round habitat.

It is possible that the Acorn Woodpecker passed through a stage resembling that of the Lewis' and Red-headed Woodpecker. It would take little modification in the existing behavior of either the Red-headed or Lewis' Woodpeckers to produce a social system like that of Acorn Woodpeckers or *vice versa.* In fact in some localities where Lewis' Woodpeckers do not migrate, a pair may remain together through the winter and store communally (Bock 1970).

If the analysis of Acorn Woodpecker sociality presented in the preceding pages is correct, it may be possible to suggest reasons for the similarities and differences among the exploitation and social systems of Acorn, Lewis' and Red-headed Woodpeckers. The question is: if the foods eaten and the ways of handling them are similar in these species, what factors have promoted convergence between the Lewis' and Red-headed Woodpeckers and divergence in the Acorn Woodpecker?

Bock (1970) has described Lewis' Woodpeckers as "opportunistic." The birds move seasonally to areas where food is abundant. If a particular area supports a sufficient amount of both winter and summer food, they are resident. The same pattern is followed by Red-headed Woodpeckers. It may be that Red-headed and Lewis' Woodpecker exploitation systems are similar because both are geared to habitat in which food is often locally abundant but annually not predictable, while the Acorn Woodpecker exploitation system is geared to habitat in which food is both locally more abundant and annually predictable. Although the data necessary to test this hypothesis are unavailable, Bock and Bock (1974) provide some evidence that supports it.

They found that the northern distribution of the Acorn Woodpecker both in the Pacific Northwest and in the Rocky Mountain region coincides not with the limits of oaks but "with those points where oak diversity drops to only one common species." The suggestion here is that the probability "of acorn crop failure in an oak community should vary in some inverse way with oak species diversity." Where only one oak species occurs, the predictability of future acorn crops is low, and such areas are not amenable to the type of exploitation system used by the Acorn Woodpecker. Lewis' Woodpeckers inhabit areas in which only one oak species occurs, presumably because their adaptation is to exploit abundant but unpredictable acorn crops. In areas where Acorn and Lewis' Woodpeckers coexist Bock (1970: 59) states "*Asyndesmus* do not ever appear to be free from competition with *M. formicivorus*, but by wintering in those areas where mast is very abundant the level of this competition may be reduced to the point where coexistence is possible." At Hastings in good mast years competition between the woodpeckers and other species was minimal. It was only when the mast crop was very patchy or poor that interspecific interactions were frequent. Consequently in years with sufficient acorns for both, Lewis' and Acorn Woodpeckers could coexist and exploit the same crop if sufficient storage facilities exist.

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SUMMARY

The Acorn Woodpecker is a sedentary species that lives in year-round groups, and breeds and stores food cooperatively. Its range extends from the western United States to northern Colombia. In California, it is most commonly found in association with oaks in oak woodland, coastal forest, and montane forest.

Observations of two groups near Orinda, California, and about 60 groups at the Hastings Reservation in central California served as the basis for most of the information presented. At Hastings 149 woodpeckers were banded and their fates followed. The preferred habitat at Hastings is foothill woodland, the savanna extension of savanna-grassland, and riparian woodland.

At Hastings groups ranged in size from 2 to 15 individuals, averaged 5 to 6, and included individuals of both sexes and all ages. Males slightly outnumbered females (1.2:1).

The Acorn Woodpecker has abandoned the typical feeding habits of its family. It feeds extensively on green acorns in late summer and autumn. It stores acorns in the autumn and feeds on these through the winter. Most group members participate in storage and all feed on the stores. It also feeds on sap and insects. Sap is obtained in a manner similar to that of sapsuckers. All group members participate in sap hole construction and all feed at them. Insects are caught on the wing. Sap and insects are important food sources from late winter or early spring through the summer. Nestlings are fed almost entirely on insects.

Each group maintains a year-round, all-purpose territory. At Hastings territories ranged in size from 3.5 to 9 ha. All group members except young fledglings defended the territory from conspecifics of other groups. Territory size is probably determined by the nutritional requirements of the group. It correlated with group size and is approximately the size of territories found in similar sized omnivorous birds.

The members of each group defended their granaries, sap trees, the trees from which they harvest acorns, anvils, hawking perches, nests, and roosts interspecifically. Some of these areas were defended seasonally while others were defended year-round. The adults of many groups excluded juvenile members from granaries from the time that storing began in late summer or early autumn for a varying period after storage was completed. During the winter the adults provisioned the juveniles by taking acorns to them on other parts of the territory.

The Acorn Woodpecker under most conditions classifies as a distance species; individuals seldom make physical contact. Acorn Woodpeckers never mutually preen. The members of each group form a dominance hierarchy. Rank is correlated with age and sex.

Acorn Woodpeckers breed cooperatively. That is more than a pair attend the nest. Presumably mating takes place among group members, but the exact mating system was not discovered. Groups did not break up into pairs, with each pair mating and laying eggs in a communal nest as occurs in some group-living species. It is presumed that older and more dominant individuals mate, but whether this involves only a pair or several individuals was not determined. Each group usually has one nest at a time in which the majority of group members aid in incubating, brooding, and feeding the young. Birds 2 years old and older are more active attendants than 1-year-olds. Once the young have fledged, the older birds continue to feed them. Young are dependent on the adults for food for several months after fledging. Under certain conditions dependency lasts almost a year.

At Hastings the reproductive rate was between 0.2 and 0.3 young fledged per adult per year. Only about 60% of the groups bred and only about 40% of the groups fledged young. About half of the young fledged each year disappeared before reaching one year of age. Most were probably killed by hawks. At Hastings accipiters are probably the most important predators on Acorn Woodpeckers.

The age structure of the Acorn Woodpecker population in the study area was weighted toward older birds. The reproductive rate was low but the survival rate of adults seemed high. It is probable that reproductive maturity is delayed until 2 years. Young remain with their natal group for at least 1 year, but most remain longer. Group recruitment is mainly by birth. Immigration accounted for a smaller percentage. Acorn Woodpecker groups therefore appear to be family units; most members are close relatives.

Within the study area (11 km^2) there were 50 to 60 Acorn Woodpecker groups. The number of groups did not fluctuate much during the study and was almost identical each summer. The distribution of groups remained nearly the same each summer. The number of groups is determined by the availability of suitable habitat.

At Hastings the birds dispersed during two periods of the year. Autumn movement usually involved entire groups abandoning their territories because of acorn crop failure. Spring movement involved recolonization of previously abandoned territories but also involved individuals changing groups.

Factors regulating group size are unclear but some possibilities are discussed. Food supply in the form of stored acorns appears to set the upper limit of group size.

The factors leading to sociality in this species are not entirely obvious, but the Acorn Woodpecker probably passed through a stage in social organization similar to the social systems of Lewis' and Red-headed Woodpeckers. The Acorn Woodpecker is probably closely related phylogenetically to these species, and it is similar to both in some aspects of its feeding habits. It differs in its group-living habit. The Acorn Woodpecker is nonmigratory, and its adaptation to seasonally abundant and predictable but highly fluctuating foods has been to stabilize these fluctuations. In so doing by the construction of granaries and sap trees, the woodpeckers have created habitat (territories) of a very specific type. The type of modifications made are such that the territory can be progressively improved and is capable of supporting increased numbers of individuals without competition between them for food. All such modified territories are occupied. Dispersal is delayed or in some cases completely obviated in the face of strong competition for territories.

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APPENDIX I. DISPLAYS

This section describes the vocal and visual displays of the Acorn Woodpecker, the stimulus situations eliciting them, and the responses to them. Displays can be defined as those behaviors, scents, and structures the function of which are to act as stimuli that effect selective responses in other organisms. We cannot state precisely the total number of vocal and visual displays used by Acorn Woodpeckers because many displays intergrade. It should be kept in mind that the repertoire described here forms only a part of the information that these birds use in integrating social relationships (Crook 1963, Hinde 1973).

The structure of each call can be seen in the audiospectrograms (Figs. 33–39). Calls differ not only in pitch but in amplitude and in spatio-temporal patterning. Some calls are given once or at most repeated two or three times in quick succession and others are typically given as a series. If a call is repeated, the interval between repetitions may be constant or variable. Some calls that are repeated are seldom if ever interrupted by other calls. Others may be broken by calls of other types and resumed. Many calls grade into other calls. A continuum exists between "different" calls. The different calls along the continuum appear to elicit different responses.

The visual displays of Acorn Woodpeckers are also variable. They may be given singly or repeated. Most vocal displays have an accompanying visual display but either may be given alone.

Tape recordings were made on a Uher 4000 Report L and a Miracorder PT 63A with an Electrovoice model 654 microphone at 19 cm/sec., using 75 cm and 25 cm parabolic reflectors. Audiospectrograms were made on Kay Electronics Co. Sona-Graphs at the Department of Zoology, Oxford, the Moore Laboratory of Zoology, and the Museum of Vertebrate Zoology. In cases where transliterations of the calls are possible, these designations are used in naming them.

WAKA DISPLAY

The *waka* call is the most characteristic vocalization of the Acorn Woodpecker. Each call consists of two parts as can be seen in Figures 33 and 34. The two parts show a sharp rising and falling in pitch. The *waka* call is rarely given singly but is repeated several times in quick succession. The parts are not given alone. The duration of a calling bout is related to the number of calls comprising it as the duration of each call and the interval between are more or less constant. Calling may occur at a variety of intensities; a single call, *waka*, may be given very softly, or the call may be repeated several times loudly. When given in a series, calling may terminate with the *trtrtr* call, the

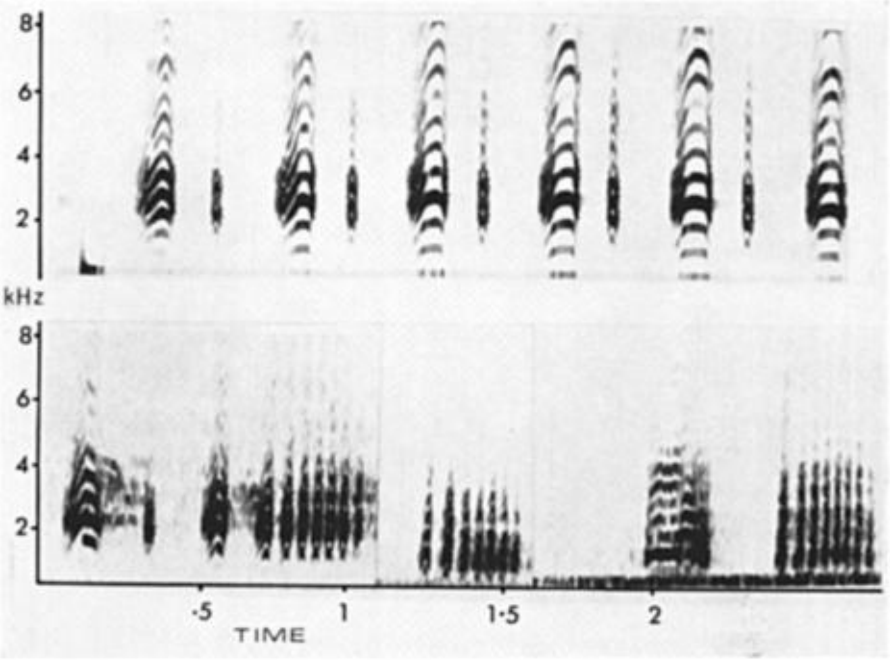

FIGURE 33. Audiospectrograms of *waka* calls (upper), *waka* calls ending in the *trtrtr* call (lower left), *trtrtr* call (lower center), and *squee-trtrtr* calls (lower right).

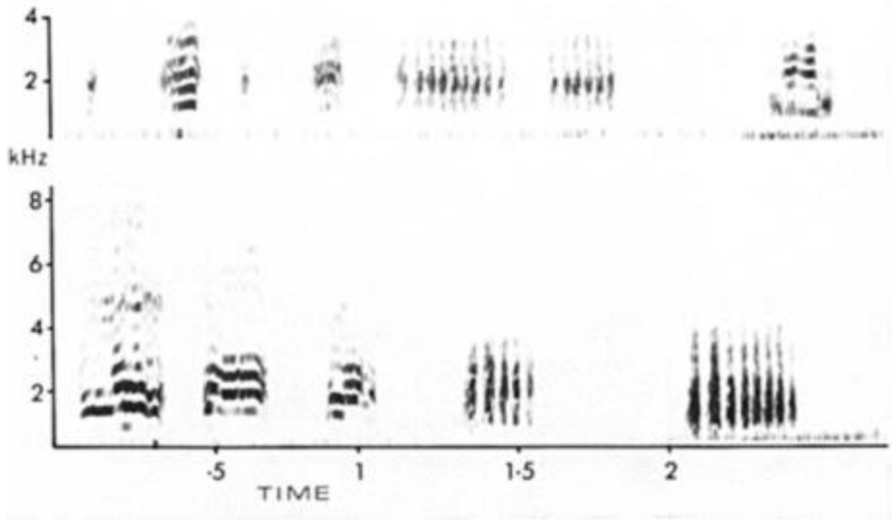

FIGURE 34. Audiospectrograms of *waka* and *trtrtr* calls (upper left), *squee* call (upper right), *squee-trtrtr* calls (lower left), and *trtrtr* calls (lower right).

typical pattern being *waka, waka, waka, trtrtr*. The *waka* call is not seasonal. Under the best conditions and at its loudest, it can be heard from approximately 0.5 km.

The *waka* call is often accompanied by a characteristic visual display. At high intensity, the visual display involves fully spread wings held open during calling. The head and tail may be slightly raised. Wing spreading is variable and grades from fully spread wings to no discernible wing movement. At low intensity, only the bill, breast, and throat move in unison with the call.

The *waka* display is given in the following contexts: (1) When one bird flies toward and lands near a member of its group, both usually give the *waka* display. Displaying generally begins before the flying bird lands and continues after landing. When a bird flies toward and lands near several members of its group, all display. It is generally the stationary bird that first displays. When several birds land close together but a few seconds apart, each displays as the others arrive. The first bird may give the display several times in succession, beginning again with each arrival.

Under the conditions described above, the *waka* display is almost obligatory. For example, when seeking cover after an aerial alarm call, individuals often perform the *waka* display in low intensity form when they land near other group members. The stationary individuals also display.

(2) The *waka* display may be given when one group member flies toward and past another group member without landing. It is generally the stationary bird only that displays.

(3) A bird being flown away from occasionally performs the *waka* display. Displaying in this case generally occurs when another bird that is being flown toward displays.

(4) An individual that is somewhat separated from its group may give a low intensity *waka* display apparently in response to other members displaying at a distance.

(5) When two or more woodpeckers are flycatching from the same tree, each time one makes a sortie and returns to a perch occupied by other birds, all may display, but if a bird makes repeated sorties that begin and end at the same perch, displaying with each flight may cease.

(6) When two birds suddenly come upon each other unaware, both may display. This sometimes occurs in nest relief but is more commonly seen when two birds on opposite sides of a tree hitch quickly to the same side.

(7) When eggs are incubated or young brooded, a bird may display when it lands at the nest entrance. Because the nest is not always occupied, a bird may display without another individual being present. If the nest is occupied, the incubating bird generally comes to the nest entrance and looks out, at which point both birds may display.

(8) An individual alone on territory may give the *waka* display. Calling in this context is often repetitive but stops when other group members return.

(9) A woodpecker may give a brief *waka* display in response to a jay or Starling landing nearby, but the display is usually cut short apparently when the woodpecker recognizes its mistake.

(10) In territorial encounters and in boundary disputes the frequency of the *waka* display increases dramatically over normal conditions. This particularly relates to the coalescing of group members into "*waka* gatherings." Several individuals belonging to the same group converge on one place, more or less simultaneously, and each individual displays. The first and second to arrive begin displaying and as others arrive displaying continues without interruption. Such gatherings become extremely noisy and once begun appear to increase in attractiveness until the entire group has assembled. Gatherings occur in quick succcession—one following another at a rate of up to three per minute. In boundary disputes the contending groups repeatedly gather on respective sides of the new

boundary. Once the boundary has stabilized, the rate of displaying slowly drops to normal level. In cases of territorial intrusion, gatherings may occur anywhere within the territory. The impression given by such behavior is that one group is attempting to "outshout" the other. In territorial fighting and boundary disputes, the threshold for displaying is lowered and almost any movement, even short flights or hopping toward another group member, may stimulate displaying.

The frequency of the *waka* display is associated with the instability of the situation. A single intruder on a territory does not lead to a dramatic increase in displaying unless the intruder persists in remaining and cannot be chased out. If several intruders are present and cannot be chased out, the frequency of *waka* display is very high.

Residents and intruders do not *waka* display to each other. It is only after an intruder has been accepted into a group that the residents *waka* display to it. Most of the initial *waka* displays in such cases are begun by the intruder, but it begins doing so only after residents have essentially ceased attacking it.

When one woodpecker flies toward and lands near a group member there are several contexts in which the display is not given: (1) When feeding nestlings at the nest entrance, an adult does not display when it flies toward and lands near them.

(2) The *waka* display is never given to a conspecific of another group. This only occurs when outside individuals have been accepted into the group.

(3) Young juveniles up to 2 to 3 months of age very often do not perform the *waka* display when they fly toward and land near another group member, and they do not often display when approached by another individual. Juveniles give the display most frequently when joining or when joined by another juvenile (but not invariably here).

(4) The display generally is not given unless the approach is by flying, except as indicated in territorial and boundary disputes or when two birds suddenly confront each other. The display may be omitted if the approach flight is short and the birds have previously been in visual contact.

(5) While flycatching, the *waka* display may be omitted even though the birds repeatedly fly toward and land near one another.

(6) In many instances the birds do not display, even though the stimulus appears to be appropriate.

The usual stimulus situation(s) eliciting the display are: approaching or being approached by a group member usually by flying, and the display itself. The response of others to the display is more difficult to delineate. The usual response is to display similarly. The function of the display is not clear and will not be speculated upon here.

KARRIT-CUT DISPLAY

The structure of the *karrit-cut* call can be seen in Figure 35. It consists of two parts. The first may be given without the second, but the second is almost invariably preceded by the first, although it may be repeated (e.g. *karrit-cut-cut-cut*). The call is frequently given as a series, *karrit-cut, karrit-cut, karrit-cut.* Calling rate may be variable or constant. The rate of calling, the number of repetitions, number of parts, loudness, and accompanying visual display all seem important. The *karrit-cut* call is nonseasonal. It can be heard at about 0.5 km.

Typically the call is accompanied by a conspicuous visual display, but the visual display may be given silently. It consists of a bobbing motion of head and body in synchrony with the call. The downward bob is timed to the *karrit;* the upward movement coincides with *cut.* Bobbing may accompany only the *karrit,* the upward movement being made with no associated vocalization. During bobbing the crest feathers may be raised.

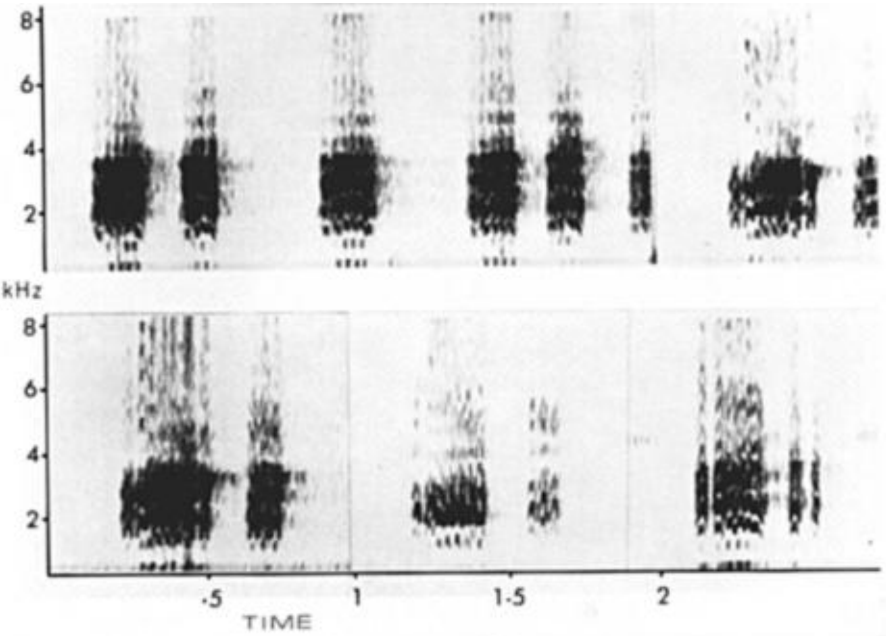

FIGURE 35. Audiospectrograms of adult *karrit-cut* calls (upper left), a juvenile *karrit-cut* call (upper right), adult *karrit-cut* calls (lower right and left), and a juvenile *karrit-cut* call (lower center).

The *karrit-cut* call grades into both the *trtrtr* call and the alarm call. Ontogenetically the *karrit* call develops from the juvenile *trtrtr* call.

The contexts in which the *karrit-cut* display is given are the following: (1) Conspecific intrusion often elicits the *karrit-cut* display by resident birds. Displaying generally begins on the intruder's arrival and continues until it has left the territory. Residents may approach the intruder and sit nearby while displaying, or they may display in flight while chasing the intruder.

(2) Intruders may *karrit-cut* display.

(3) The woodpeckers frequently *karrit-cut* display in response to birds of other species and mammals in those areas of the territory that they defend interspecifically. The woodpeckers may approach such intruders and display while stationary or they may display while chasing them.

(4) The display may be given in response to flying hawks or owls. More usually however the alarm call is given, but any call intermediate between it and the *karrit-cut* call may be given.

(5) A hawk or owl sitting within the territory often elicits a *karrit-cut* display. The woodpeckers may fly repeatedly at such individuals while displaying but more commonly they display at a distance. If the hawk or owl remains in the area for some time, displaying wanes and may even cease. In one case in which a woodpecker was caught by a hawk, the other members of its group sat in a tree nearby giving *karrit-cut* displays.

(6) *Karrit-cut* displays frequently occur for a short period just after the members of

a group have left their roosts in the morning and just before they enter their roosts at night.

(7) The display is sometimes given by a woodpecker when approached closely by a human.

(8) A bird alone on territory may occasionally give this display.

(9) The display is often given at the end of the silent period following an alarm call. When an alarm call has been given, the woodpeckers may hide in roost holes. After the silent period, the first and often the second individual to leave the hole may quickly fly to a nearby branch and vigorously *karrit-cut* display.

(10) When a bird that has been incubating or brooding leaves the nest without being relieved, it may fly to the top of a nearby tree and *karrit-cut* display. This apparently only occurs if the individual is not in visual contact with other group members.

(11) When a hawk flies at a woodpecker, the woodpecker usually takes flight, often upward in a zigzag pattern. In flight the bird may *karrit-cut* call. In such cases the vocalization tends to be *karrit-cut-cut-cut.*

The stimulus situations eliciting this display are the presence of potential predators and conspecific or heterospecific intruders. The response of other group members to the display is (1) attend to the source of the display, and (2) approach the source of the display. When mobbing a potential predator, conspecific or heterospecific intruder, it is not clear what the effect of the display is on group members or intruders. It may be that the display deters or hastens the retreat of intruders, but as the display is often accompanied by other behaviors, it is not possible to demonstrate this. In situations 2, 6, 8, 9, and 10, further comment is necessary. The function of displaying by conspecific intruders is not clear. The variables involved in these situations are so numerous that it was not possible to correlate the display with any particular response on the part of others. Numbers 6, 8, 9, and 10 all have similarities; 6, 9, and 10 are associated with leaving (and 6 also with entering) roosts and/or nests. In these cases the bird usually is not in vocal or visual contact with other group members and is leaving the hole "blind," that is it does not know the situation outside. In cases 8 and 9, the calling bird is very often out of visual and auditory contact with other group members.

ALARM CALL

Audiospectrograms of the alarm call can be seen in Figure 36. It is structurally similar to the *karrit* call and these two calls intergrade. The alarm call appears to develop from the *trtrtr* call and does not appear to be present in the juvenile repertoire until about 2 months after fledging. It is nonseasonal and can be heard at about 0.4 km. No conspicuous visual display accompanies the call.

The eliciting stimulus for the alarm call is usually a flying hawk, typically an accipiter or buteo. The woodpeckers occasionally make mistakes and give the alarm call when rapidly approached by nonpredatory birds such as band-tailed pigeons (*Columba fasciata*) and turkey vultures (*Cathartes aura*). They may also give alarm calls when suddenly confronted with a human close by, as when an observer leaves a blind.

The alarm call typically is given only once or twice, but it may be repeated several times in quick succession. The interval between calls is variable.

The response to an alarm call can best be described as "taking cover." An individual may simply freeze, quickly hitch to the underside of a limb and remain motionless, or make a quick dash for the nearest roost hole. After an alarm call has been given, a period of silence follows during which the woodpeckers remain motionless. Presumably the duration of this period is related to the length of time the eliciting stimulus is present. In some cases, as when inside a roost, the woodpeckers have no way of knowing whether

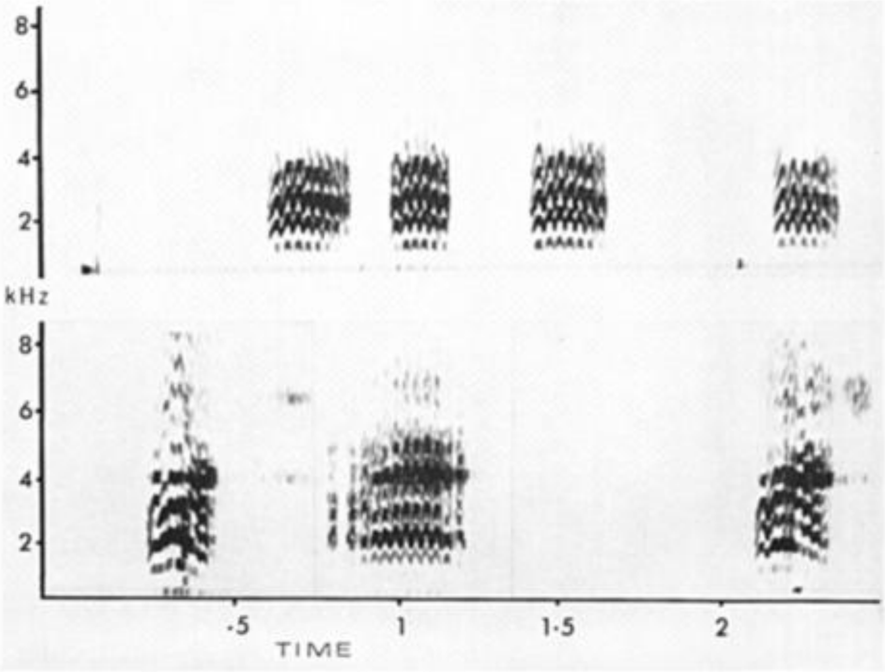

FIGURE 36. Audiospectrograms of alarm calls (upper, and lower right and left), and a fledgling *karrit-cut* call (lower center).

or not the eliciting stimulus is still present and the length of the silent period must be determined by other factors.

The woodpeckers respond to the alarm calls of members of other groups on adjacent territories in the same manner as to alarm calls given by group members. Other animals, particularly some birds of other species and Ground Squirrels, respond to Acorn Woodpecker alarm calls by taking cover. The call is undoubtedly an anti-predator adaptation, but it is not clear if it functions to elicit hiding by members of other species as well (Trivers 1971).

URRK DISPLAY

The structure of the *urrk* call can be seen in Figures 37 and 38. The call is usually given singly but may be repeated two or three times in quick succession with a variable interval between calls. It may also be given as two parts, *urrk-uk*, but this is rare. The *urrk* call grades into the *waka* call, and calls intermediate between these are frequently given. For example, a bird may begin a bout of *waka* calls, but with each repetition the call assumes a more *urrk*-like structure until the final calls in the series are *urrks*, usually of the two-part type.

The *urrk* call occurs year-round, but it is most common in the spring and early autumn. It is not loud and can be heard at about 0.2 km.

A characteristic visual display often accompanies the call. A calling bird may raise its crest feathers, raise its breast and hop forward or, while stationary, it may assume a raised

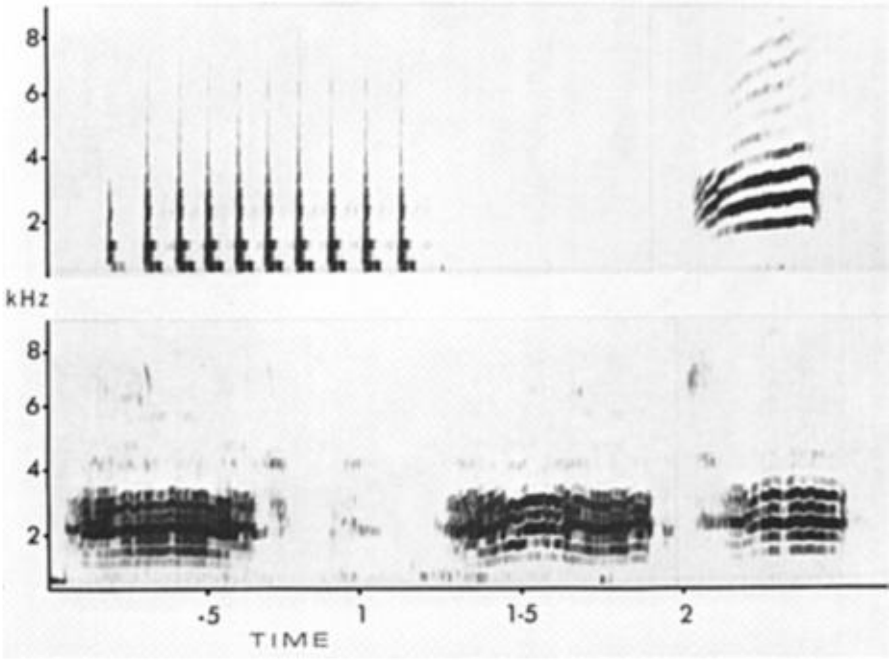

FIGURE 37. Audiospectrograms of drumming (upper left), a *garrick* call (upper right), and *urrk* calls associated with feeding young at the nest entrance (below).

breast, bill-down posture with crest feathers raised. The body feathers are sometimes fluffed. The call may also be accompanied by another posture in which the crest feathers are raised and the head thrust forward with the bill pointing directly ahead in line with the body. When calling at low intensity, a bird usually only raises its crest feathers.

The *urrk* display occurs primarily in four contexts: (1) Sometimes it is given by a resident woodpecker just prior to flying at a conspecific intruder. The display is given only when the resident and intruder are in close proximity. More rarely, the resident bird gives the *urrk* display when chasing an intruder in flight. The display is not given by the intruder.

(2) The display is occasionally given by adults when feeding nestlings at the nest entrance. It is usually given after rather than before the adult has transferred food to the young and just before it flies from the nest.

(3) The *urrk* display may be given by an adult when feeding young fledglings. Juveniles often crowd adults when food begging and adults may respond to such importunities by pecking them and giving an *urrk* display.

(4) In groups in which the young are kept from granaries during the storage season, adullts may perform the *urrk* display when attacking juveniles that enter the granary.

The function of the *urrk* display is not completely clear. As it is usually given just before a bird flies at an intruding conspecific, it probably has little to do with providing information to other group members about the presence of an intruder. Usually other group members have been aware of the intruder through other displays, or they have

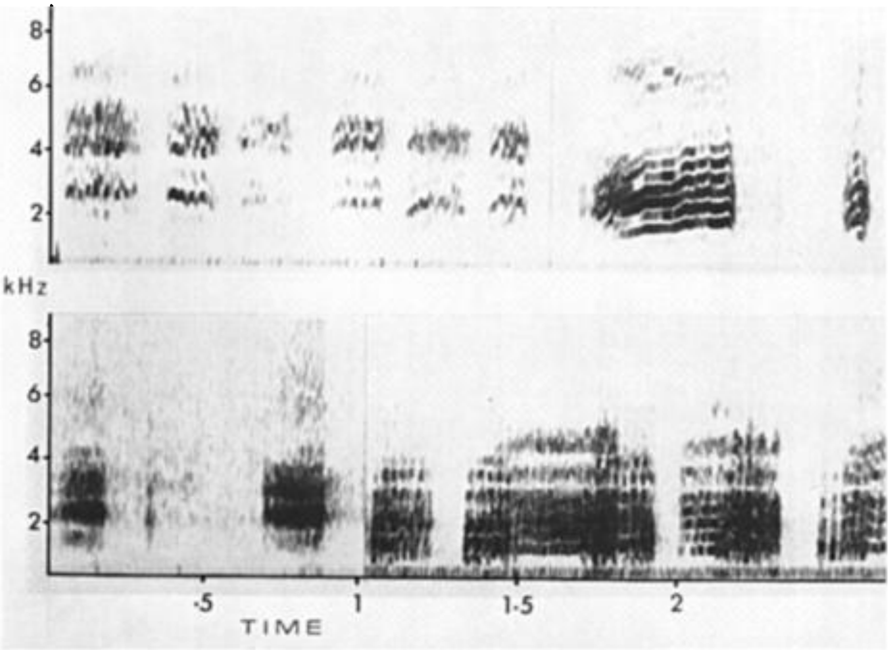

FIGURE 38. Audiospectrograms of chatter calls (upper left), *urrk* calls (upper right and lower left), and *squee* calls of a young bird begging (lower right).

already seen the intruder themselves. The intruder's reaction to the displaying individual is to fly immediately after the display is given but before the resident bird has flown toward it. If the resident displays and the intruder does not fly, it usually is flown at. When the display is given while feeding young at the nest, it does not appear to elicit any noticeable response from them. The adult is in close proximity to a strange bird, but such situations never involve pecking or attack. Of the remaining contexts, those in which a young bird is pecked while begging food from an adult or is chased when entering a granary, too many other variables are involved to determine if the display itself produces any particular response. Young birds when attacked by adults that give the *urrk* display do not seem to respond differently from when they are attacked silently.

GARRICK DISPLAY

The structure of the *garrick* call can be seen in Figure 37. It does not appear to grade into other calls. It may be given as a single utterance, but more commonly it is repeated with a variable interval between calls. Calling is generally accompanied by an inconspicuous forward head movement. The *garrick* call does not appear to be present in the juvenile repertoire for at least 3 to 4 months after fledging, but exactly when it first appears is not known. Although the display may be given at any time of year, it is most common during the spring. It can be heard up to about 0.5 km.

The *garrick* display typically occurs in four contexts: (1) Resident birds may give the *garrick* display, often repetitively, when a conspecific intruder is on their territory.

Displaying ceases when the intruder leaves. Unlike the *urrk* display, the *garrick* display is not associated with the act of chasing an intruder, and a displaying bird need not be close to the intruder. The display is given while the performer is stationary.

(2) Although intruding conspecifics are usually silent, they may *garrick* display. The display is generally accompanied by other displays, specifically the *karrit-cut* display and drumming.

(3) An individual may give this display when alone on territory or when most of its group are absent. It stops calling when other group members return.

(4) The display is sometimes associated with nesting. In one group that lost two nests, the single adult female *garrick* displayed after the first nest was lost and again after the second loss. After the first loss, the members of the group began to refurbish a second nest and during the several days that this required, the female frequently *garrick* displayed both from inside and outside the nest. The rate of displaying dropped once incubation had begun and ceased when incubation was regular. After the second nest loss, the female again performed *garrick* displays in the area of the old nest and began to refurbish yet another nest. Both displaying and refurbishing soon ceased and no new clutch was begun. After the second nest was lost, the female was almost always alone in the area of the nest; the two males spent no time at the old nest and took no part in refurbishing the new one.

The *garrick* display occurs in other situations that appear similar to those described above. An incubating bird may give *garrick* displays from inside the nest when other birds give *waka* displays nearby.

The response of other group members to this display is variable, and like many other displays, the *garrick* display is often accompanied by displays of other types, which confuse the issue. The usual response to the display is to stop activity and look around. The respondent often flies to and joins the displaying individual. In cases involving conspecific intrusion, displaying may result in alerting other group members to the intruder's presence. When the display is given by the intruder, its effect on other individuals is difficult to separate from other variables as both residents and intruders may perform *garrick* displays simultaneously. The function of the display in situation 3 and 4 is difficult to suggest. But as the display occurs mainly in the spring, this suggests that it is in some way related to reproduction, but how we do not know.

DRUMMING

Drumming has been described for a number of woodpeckers. It is an instrumental sound produced by striking the bill against (usually) wood and is often executed on specific drumming posts, typically dead limbs with good resonance.

The structure of a single tap in drumming does not differ from tapping under normal circumstances; it is the temporal ordering of taps that distinguishes drumming (Fig. 37). In the Acorn Woodpecker, both sexes drum. Each drumming bout consists of from 2 to 20 evenly spaced taps. When an individual gives a series of drumming bouts, the interval between each usually varies. Drumming in the Acorn Woodpecker differs from drumming in some woodpeckers in which the usual pattern is a long series of bouts with a standard interval between each. Although drumming may occur at any time of year, it is most common in this species in the spring. It can be heard up to about 0.5 km.

Drumming occurs in two contexts: (1) It is most often associated with intraspecific territorial encounters. It is usually given by residents only. (2) When alone, a woodpecker may drum. In such situations, which are not common, the bird may also *garrick*, *waka*, or *karrit-cut* display.

Drumming in other woodpeckers appears to have either courtship or territorial functions or both. A bird drumming is said to attract a mate and to repel conspecifics of the same sex. In the Acorn Woodpecker, it is correlated with intraspecific intrusion, especially in the spring, but in what ways it affects the behavior of other group members or the behavior of intruders is not at all clear. When a bird drums, it or other individuals are usually giving other displays as well. Context alone indicates that drumming probably is directed at intruders and may hasten their retreat. As drumming is largely confined to the spring a reproductive function may exist, but what this may be remains unknown.

CHATTER DISPLAY

The structure of the chatter call can be seen in Figure 38. It is usually given as a repetitive series. The interval between calls may be constant or variable. It is nonseasonal and is audible up to about 0.2 km.

The chatter call is an intragroup call. It is given most frequently just before, during, and/or just after one individual has attacked another group member. The bird being attacked gives the call. The call is also occasionally given when two birds are in close proximity (often touching) but without attack being involved. Less often the call is given by a bird that, when in close proximity to other individuals, is likely to be attacked.

The chatter call is accompanied by a characteristic posture. The calling individual either turns away from its attacker and freezes with head raised and crown feathers flattened or assumes a hunched posture with head withdrawn and bill pointed downward. As the attacking bird generally aims pecks at the other's head, by turning away the bird being attacked reduces the severity of the attack. Most pecks can be directed only at the nape. Although a bird usually utters chatter calls when attacked, this is not invariable. The hunched face-away posture however usually is assumed in an attack. This posture may also be assumed by one individual when in close proximity to another without an attack being involved. Like the call, the associated postures are variably expressed—from the most intense form described above to simply facing away. When severely attacked, an individual may fly from its assailant, but this is unusual.

In all situations in which one individual attacks another, it is the dominant bird that is the attacker, and in all cases, it is the subordinate that performs chatter display. Youngsters excluded from granaries often give the chatter call if they enter a granary. A young bird may even chatter as it flies toward a granary and continue to call after arrival. After they are allowed into the granary, young birds often give chatter calls, particularly when in close proximity to adults. Chatter calls may be given when two birds suddenly come upon each other. For example, during nest relief when one bird enters the nest before the other has left, the subordinate may chatter. The call often is given by a bird begging food from another. The begging individual, which is always the subordinate, may attempt to get close to the bird with food and may chatter and also give the *squee-trtrtr* call. Such individuals are often pecked.

Various features of the contexts of the chatter call point to its function. It is exclusively an intragroup call given by subordinate individuals and probably functions to prevent or to reduce the severity of attack.

SQUEE AND *TRTRTR* DISPLAYS

The following two displays are considered together as they are closely associated in the juvenile repertoire and only later become disassociated.

The *squee* call is one of two vocalizations typical of older nestlings and juveniles. Its structure can be seen in Figures 33, 34, and 38. The call may be repeated without interruption by other calls, but it is usually followed by one or more *trtrtr* calls in the pattern *squee, trtrtr, squee, trtrtr, trtrtr.* When given repeatedly, the duration between calls may be either constant or variable. It can be heard at about 0.2 to 0.3 km. The call, although present in both juvenile and adult repertoires, is seldom given by adults. It is not clear if the *squee* call develops into any of the adult vocalizations, but it is possible that the chatter call is a modified *squee* call.

The structure of the *trtrtr* call can be seen in Figures 33 and 34. The call consists of up to 9 or 10 quickly repeated vocalizations. The *tr* is similar structurally to the second part of the *waka* call. It can be heard at about 0.2 to 0.3 km. Young birds usually give the *trtrtr* call in conjunction with one or a series of *squee* calls. Unlike the *squee* call, the *trtrtr* call does not drop from the birds' repertoire with age but rather (1) it differentiates into other calls, (2) is retained in its original form and context but is seldom used, and (3) is retained in its original form but is used in different contexts.

The *karrit* and alarm calls develop from the *trtrtr* call. This occurs over a period of weeks and begins when juveniles are about 1 to 2 months old. Juveniles initially never give clear adult-type *karrit* and alarm calls but only calls intermediate between them and the *trtrtr* call. These calls are often ambiguous, and it is only by context that they can be distinguished from alarm or *karrit* calls. For example, we observed that often when young birds *karrit* called all other group members immediately hid, the typical response to an alarm call. But once this transitional phase has passed, typical *karrit,* alarm, and *trtrtr* calls can be distinguished. Nevertheless, in the adult repertoire all gradations between these three calls may occur and the types only remain parts of a continuum, of which certain parts are emphasized.

When adults *trtrtr* call, the call generally is given independently of other calls but may follow other calls. It is given as a single utterance or repeated several times. The interval between repetitions is variable or constant.

Like other calls, the *squee* and *trtrtr* calls have a variable intensity (loudness, frequency of repetition) of expression as do the visual displays associated with them. Call and posture intensity are correlated. At one extreme the *squee* call may be given very softly, without repetition, and with no discernible visual display. At the other extreme it may be given with feathers raised, especially on the head, and a bobbing movement. In the least intense form of the *trtrtr* call only a vibrating of the throat is noticeable, but at high intensity it may be accompanied by quick head bobbing, very rapid wing flicking, and feather erection, especially on the head. In a normal sequence at high intensity, juveniles usually intersperse *squee* calls with *trtrtr* calls. When the *squee* call is given by adults, the form of the accompanying posture is the same as when it is given by juveniles. The adult *trtrtr* call, although identical to the juvenile call structurally, is usually given without the visual display.

The *squee* and *trtrtr* displays are commonly given in the following contexts: (1) When nestlings reach the age at which they can look from the nest hole, these two calls, interspersed, may be given almost continuously. When an adult approaches the nest, the intensity of displaying increases. While eating, the young give the *squee* display repeatedly. When the adult leaves, the intensity of displaying drops to the pre-feeding level.

(2) Fledged young give the *squee-trtrtr* displays when being fed by adults. Young birds may also give the displays in flight when following an adult from perch to perch and when sitting near an adult. They may display when alone, but the visual displays are seldom given in this context.

(3) The young often give these calls in a context similar to the *waka* display. When an

adult flies toward and lands near a juvenile or vice versa, the juvenile gives a series of *squee-trtrtr* displays.

Although both displays are retained in the adult repertoire, the *squee* call is given only in combination with the *trtrtr* call. The combined *squee-trtrtr* display is given only during begging (a rare occurrence) or very occasionally when an adult is in close proximity to another adult. The *trtrtr* call is given by adults in several contexts: (1) It often follows a series of *waka* calls and may be repeated several times in succession.

(2) A lone adult may call *trtrtr* when other members of the group give a *waka* display at a distance.

(3) Resumption of normal activity after the silent period following an alarm call may be preceded by one bird giving a *trtrtr* call followed by other members of the group giving this or other calls.

(4) An adult may call *trtrtr* in "reply" to other birds that give the call. That is, one individual calls *trtrtr* and another bird, either at a distance or within the visual field of the calling individual, replies.

(5) A bird may call *trtrtr* when alone.

The functions of these displays can be sugggested. The combined *squee-trtrtr* display is given when one member begs for food and/or when it is fed by another group member. This usually involves juveniles begging from adults, but adults occasionally beg from other adults. Displaying may facilitate approach and therefore being fed. The function of the *trtrtr* display once it has become disassociated from the *squee* display is less clear. As the *trtrtr* call grades into the *karrit* call and the *karrit* call is often associated with some disturbing situation, it may be reasonable to suppose that the *trtrtr* call has a similar relation to disturbing stimuli, but only those of mild nature. Its effect on other group members is difficult to assess except that *trtrtr* calls are frequently responded to with other *trtrtr* calls.

TSE AND RASP CALLS

Young nestlings give two vocalizations. The structure of these can be seen in Figure 39. The *tse* call involves clear notes. The rasp call is a harsh noise, given over a wide range of frequencies with no clear structural breaks. When these calls first appear is not clear. The *tse* call probably develops before hatching and the rasp after hatching. Both appear to drop from the repertoire before fledging, but they may develop into the *squee* and *trtrtr* calls.

The *tse* call is characteristic of very young nestlings and is given continuously when they are alone in the nest. The only cessation in calling occurs when the rasp call is given or when the young are being brooded. As they develop, they cease calling in this manner and remain quiet much of the time. The *tse* call can be heard at 15 to 30 m; the rasp at about twice this distance.

The rasp is given when an adult lands at the nest entrance and enters the nest. Calling continues as long as the adult is in the nest, unless it broods the young, and may continue for a few seconds after the adult has left. When nestlings are very young, a simple darkening of the nest is sufficient to elicit the call. As they develop, this no longer elicits the call, but by putting a twig down into the cavity and presumably touching the young, calling can be stimulated. After a period of time only an adult entering the nest elicits the call. When nestlings are still young, the rasp call is occasionally given when they are alone in the nest. Calling in this case may result from tactile stimulation among the nestlings themselves.

The functions of the *tse* and rasp calls are not clear, but they may facilitate feeding. Additionally, the rasp call shows some similarity to rattlesnake rattling. Many hole-

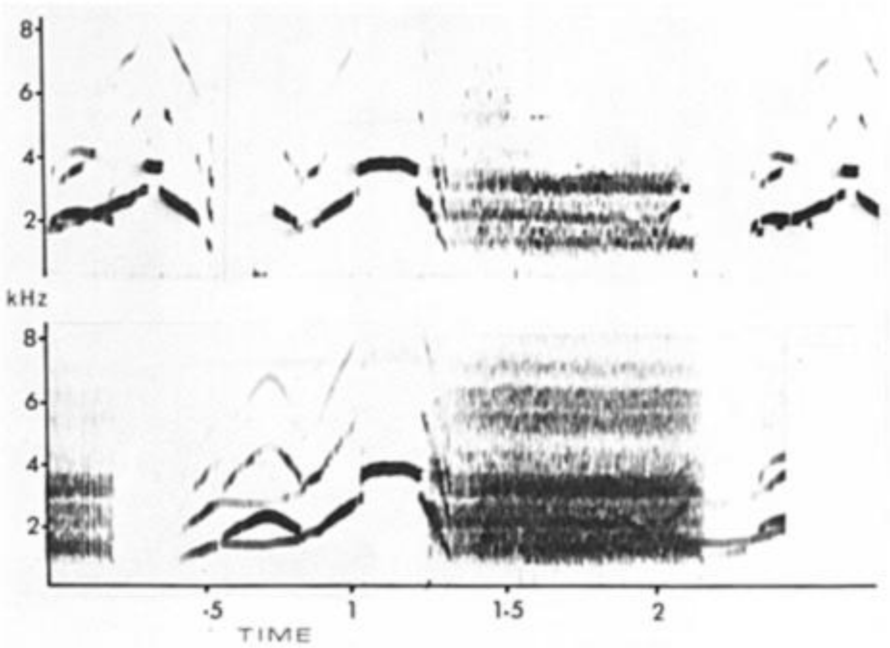

FIGURE 39. Audiospectrograms of *tse* and rasp calls.

nesting birds have vocal displays that are said to resemble or mimic snakes hissing or a rattlesnake rattling (Sibley 1955, see audiospectrograms in Martin 1973). As we did not observe any encounter between nestling Acorn Woodpeckers and other species, we cannot say whether or not the rasp call functions to deter potential predators.

PRE-ROOST MOUNTING

The woodpeckers engage in a type of mounting behavior that is neither seasonal nor a prelude to copulation. Mounting occurs at specific localities within the territory just before the birds retire to their roosts in the evening. The entire group, or a large part of it, assembles and often sits quietly for a few minutes; one bird then hops over to another and mounts it. Mounting may involve any group member mounting any other. Males mount females and other males; females mount males and other females. As it was usually quite dark when these interactions occurred, it was difficult to read leg bands. Yet from what we were able to see, mounting does not appear to be age related; young birds mount older birds and vice versa. Mounting is very brief and does not involve cloacal contact or any special movements of the tail. It may be very perfunctory with one bird simply treading on the wing tips and tail of the other. Two birds may execute a quadruple mount in which each mounts the other twice in turn. There does not seem to be any vocalizing involved in these interactions. In most cases reverse mounting occurs, in which one bird mounts and is mounted in turn. Mounting may be followed by a brief period in which the birds sit quietly or they immediately fly to their roosts. The function of mounting in the above context is not known, but it certainly does not appear to be related to copulation.

SCREAM CALL

The scream call is given either as a continuous call or as a series of short calls with a variable but usually short interval between calls. The vocalization consists of noise over a wide range of frequencies but especially in the 1 to 6 kHz range. The call is present in the nestling repertoire about a week before fledging. It is not seasonal and can be heard up to about 0.5 km.

We observed the scream call in four contexts, all involving physical contact between the individual calling and another individual.

(1) It may be given during intergroup territorial fighting when two woodpeckers of different groups make contact and grapple. In such situations it was not possible to determine which individual called; perhaps both did.

(2) On one occasion, the call was given repeatedly by a woodpecker that had been caught by a Cooper's Hawk.

(3) On one occasion, a woodpecker was chased by a pair of bluebirds, and while in flight, one of them momentarily grappled with the woodpecker. The woodpecker gave the scream call.

(4) The scream call is frequently given, often repeatedly, when a human handles a woodpecker. Such a captive ceases calling as soon as it is released or placed in a holding cage. When we handled a screaming woodpecker other group members, and birds of other species, sometimes approached, but they soon dispersed and were silent. In number 2 above, the other members of the group assembled in a tree nearby and repeatedly *karrit-cut* displayed. *Karrit-cut* displays never occurred when we handled screaming birds. In the other cases mentioned, the encounters between woodpeckers and other individuals were too brief to determine whether the call elicited any response from other group members.

Although the function of the scream call is not entirely clear, it appears to produce two responses: one from members of the group, which come to investigate and/or hide, and another from antagonists upon whom the call may have a disconcerting effect.

APPENDIX II. INDIVIDUAL AND GROUP HISTORIES

The members of each group are listed with each individual's reference code (based on color bands), sex, age when banded or first observed, date when banded or first observed, and history after banding. Below the membership list is a short vignette of each group's history. A key is given below:

> N = nestling; A = adult (over 1 year of age); J = juvenile (less than 1 year of age); b. = banded; p. = present; r. = residing in group when study terminated in August 1974; d. = disappeared from study area but fate of bird unknown; k. = killed; m. = moved to another group; f. = fledged; Unbanded = Unbanded bird.

GROUP 1

LBRY	♀	A	b. 1 Oct. 1972	r.
RM	♀	J	b. 30 Sep. 1972	r.
Unbanded	♂	A	p. 30 Sep. 1972	r.
Unbanded	♂	A	p. 30 Sep. 1972	d. spring 1974
Unbanded	?	J	f. July 1974	r.

This group was first observed and two females banded in the autumn of 1972. One of the females was a juvenile presumably fledged in the group in the summer of 1972.

The two others were males judged to be adults. The group bred in 1973, but the nest failed after the eggs hatched. In early September 1973 the group abandoned their territory because of acorn failure and moved to an area near groups 2 and 4. Here they occupied an area that had not been used previously by Acorn Woodpeckers. They stored in several trees, mainly under loose bark and in desiccation cracks. They made a few storage holes. They overwintered in this area but abandoned it and moved back to their old territory in late April 1974. After the move, one of the males disappeared. The group bred in 1974 and fledged at least one juvenile.

GROUP 2

WP	♂	A	b. 19 Oct. 1971	r.
Unbanded	♀	A	p. Oct. 1971	r.
WBY	♀	J	b. 25 Oct. 1971	d. early May 1974
WR	♀	A	b. 9 Oct. 1971	m. April 1972 to group 6
WGBl	♂	A	b. 22 Oct. 1971	d. Dec. 1971
WDB	♂	J	b. 19 Oct. 1971	m. April 1972
Unbanded	♂	J	p. Oct. 1971	d. April 1972
WPBl	♀	J	b. 25 Oct. 1971	k. 9 Nov. 1971
RDG	♀	N	b. 5 June 1972	d. May 1974
BBlW	?	N	b. 5 June 1972	d. June 1972
OR	?	N	b. 30 May 1974	r.
LGDPLP	?	N	b. 30 May 1974	d. June 1974

In late October 1971 this group consisted of eight birds: four adults and four juveniles presumably fledged in the group the previous summer. WPBl was killed by a Cooper's Hawk in November. In December WGBl disappeared, presumably also killed by a predator. No other changes occurred until April when three birds moved. One moved to group 6 and two moved out of the study area. This left three birds, one of which was 1 year old. The group bred in 1972 and fledged two young, but one soon disappeared. The group remained as four birds throughout the next year. They started a nest in 1973, but the nest failed in the egg stage. In September 1973, group 3 invaded the eastern part of group 2's territory and occupied this area until mid-November. Group 2 remained as four individuals until early May 1974 when the two youngest left after the 1974 nest had been begun. This left two birds. The 1974 nest fledged two young. One of these disappeared soon after fledging. The group contained three individuals when the study terminated.

GROUP 3

LPR	♂	A	b. 15 Sep. 1973	Not followed after Nov. 1973
LBm	♀	A	b. 11 Sep. 1973	Not followed after Nov. 1973
DPm	♂	A	b. 14 Sep. 1973	Not followed after Nov. 1973

Plus several unbanded males and females, both adults and juveniles

This group, like group 1, had no acorns on its territory in the autumn of 1973, but instead of abandoning, the birds moved daily to an area about 0.3 km away where acorns were plentiful and collected nuts there. They transported nuts from this area to their own storage tree. They displaced groups 2 and 4 from parts of their territories at this time. After the 1973 harvest they moved back to their own territory. We never made a complete count on this group, but it probably consisted of about eight individuals, some of which were juveniles. Woodpeckers lived at the group 3 territory throughout the study, but except to note their presence we made observations on them only during the late summer and autumn of 1973 when they were within the reservation boundaries.

GROUP 4

ORW	♀	A	b. 2 Nov. 1971	r.
ODBLB	♀	A	b. 2 Nov. 1971	d. March–April 1972
OGW	♀	A	b. 2 Nov. 1971	d. March–April 1972
Unbanded	♂	A	p. Nov. 1971	r.
DGY	♂	A	p. Nov. 1971, b. 15 Sep. 1972	r.
WGO	?	N	b. 26 May 1974	r.
PP	?	N	b. 26 May 1974	r.
DBRO	?	N	b. 26 May 1974	r.

In early November 1971 this group contained five birds, three females and two males, all of which appeared to be adults. The group retained the same composition until late March or early April 1972 when two of the females disappeared for unknown reasons. The group did not breed in 1972. In late August 1972 it moved to School Hill and secured a territory there. This move was prompted by acorn failure on the territory. One of the males was caught and banded in September. The old territory remained vacant through the winter, and in March 1973, the group began moving back. It frequented both the School Hill territory and the old territory through the summer but finally settled permanently in the old territory in the summer of 1973. Group 4 did not breed in 1973 although it began refurbishing one nest. The birds bred in 1974 and fledged three young, which were still with the group when the study terminated.

GROUP 5

DBPm	♂	A	b. 24 Nov. 1973	d. Feb. 1974
DBm	♀	J	b. 18 Jan. 1974	d. Feb. 1974

Plus several unbanded males and females. All disappeared in February 1974.

This group displaced group 4 from part of the latter's territory in late August or early September 1973. The history of group 5 prior to this is unknown. Its movement into this area, like that of other groups at this time (groups 1 and 3), was presumably stimulated by acorn failure at home. The group consisted of about six individuals, at least two of which were juveniles. The exact composition was not determined. It occupied an area that did not have a granary. The birds stored acorns under loose bark and in desiccation cracks in a dead willow. They abandoned the area in early February 1974 when their acorn stores were exhausted. Where they went is not known.

GROUP 6

LGRG	♀	A	b. 8 Nov. 1971	d. August 1972
LGM	♂	A	b. 19 Nov. 1971	d. August 1972
LGBlW	♀	A	b. 2 Dec. 1971	d. August 1972
LGPBl	♂	A	b. 10 Dec. 1971	d. August 1972

Unbanded	♂	A	p. Nov. 1971, b. 18 Sep. 1972	d. Sep. 1972. This bird was banded (OPOP) in September 1972 on School Hill after his group had abandoned its territory. He was recognizable by a malformed foot and some peculiarities in head feathers. When caught he was very thin. He was not seen again
WR	♀	A	b. 9 Oct. 1971 as a member of group 2	She moved to group 6 in mid-April 1972. She stayed with that group until August 1972 when she disappeared with the remainder of the group

Group 6 was banded in the autumn of 1971. It consisted of two females and three males, all adults. The group remained unchanged until April 1972 when WR female from group 2 joined it. The group, now with six birds, remained unchanged until August 1972 when it abandoned the territory because of acorn failure. Only one bird (unbanded ♂, later OPOP) was seen again. Group 6's territory remained empty until late March 1973 when two unbanded individuals occupied it. Group 6 did not breed in 1972. If a clutch was begun in that year, it was lost immediately.

GROUP 6a

Rm	♀	A	p. March 1973, b. 27 Oct. 1973	r.
YLG	♂	A	p. March 1973, b. 27 Oct. 1973	r.
GPLG	?	J	f. June 1974, b. 12 July 1974	r.
Unbanded	?	J	f. June 1974	r.

This group (a pair) occupied the group 6 territory in March 1973. Group 6 had abandoned it in August 1972 because of acorn shortage. These two individuals were banded the following October. The group's history prior to occupying this area is not known. No breeding occurred here in 1973. In 1974 the group bred and fledged two young. One of the juveniles was banded later in the summer. The group still consisted of these four individuals when the study was terminated.

GROUP 7

Unbanded	♀	A	p. Jan. 1972	d. March 1973
OO	♂	A	b. 22 Jan. 1972	d. March 1973
PWm	♂	A	b. 22 Jan. 1972	d. March 1973
GLGPBl	♀	A	b. 14 Dec. 1971	d. between March and Oct. 1972
LBLG	♀	A	b. 22 Jan. 1972	d. between March and Oct. 1972
PGLG	♀	A	b. 14 Dec. 1971	d. between March and Oct. 1972

GW	♂	A	b. 22 Jan. 1972	d. March 1973
LBDB	♂	A	b. 22 Jan. 1972	d. March 1973
DBDB	♀	A	b. 28 Dec. 1971	m. to group 12 in Aug. 1972; rejoined group 7 in March 1973. Disappeared March 1973
WW	♀	A	b. 22 Jan. 1972	m. to group 12 in August 1972; rejoined group 7 in March 1973. History after this obscure. Seen several times in summer of 1973 with group 15c. Last seen in Sep. 1973 near group 5. She was apparently a member of group 15c in the summer of 1973 but left it in late summer

Most individuals were banded in the winter of 1971–72. The group at this time consisted of four males and six females. In late March 1972 all were present. Two of the birds left the group and joined group 12 in late August 1972. By October 1972 the group composition was four males and one female. The group remained unchanged through the next winter, but in March 1973 the females that had joined group 12 rejoined group 7. Composition was now four males and three females. This continued for about 2 weeks, when the entire group with the exception of WW (see above) disappeared in late March. Group 7 did not breed in 1972, and why they abandoned their territory in 1973 is not known. Although the birds were within the 1972 freeze zone and therefore had no acorns on their territory, they managed to store a quantity sufficient to carry them through the 1972–73 winter by harvesting nuts from the upper slopes of an adjacent hill above the freeze zone. Where they went after abandonment is unknown, and only WW was subsequently seen.

GROUP 7a

LBW	♂	N	b. 9 June 1972 in group 12. Left group 12 in April 1973 and occupied area vacated by group 7	r.
Unbanded	♀	A	p. April 1973	r.
DGDP	?	N	b. 31 May 1974	r.
LGLG	?	N	b. 31 May 1974	r.

After group 7 abandoned its territory in March 1973, a pair immediately occupied it. The male was LBW, banded as a nestling the previous summer in group 12. The female was unbanded. She may have been the unbanded group 7 female. In 1973 this pair began refurbishing a nest but apparently no eggs were laid. The pair remained throughout the next winter and fledged two young in 1974. Group 7a consisted of four birds when the study terminated.

Group 8

DGLGLB	♂	A	b. 1 Dec. 1971	d. Dec. 1971
DGm	♂	A	b. 1 Dec. 1971	d. Dec. 1971
LBODB	♀	A	b. 1 Dec. 1971	d. Feb. 1973
Unbanded	♂	A	p. Dec. 1971	d. Feb. 1973
Unbanded	♂	A	p. Dec. 1971	d. Feb. 1973

Group 8 consisted of five birds in December 1971. Three were banded, but two of these soon disappeared for unknown reasons. The group did not breed in 1972. With one female and two males, group 8 occupied the area until February 1973. Although the area suffered from the 1972 freeze and subsequent acorn crop failure, it was surrounded by high hills that extended above the freeze zone and the birds were able to gather nuts and store to a limited extent. Stores were insufficient and were exhausted by February, at which time the group left. The territory remained unoccupied until April 1973 when two unbanded birds took possession.

Group 8a

Unbanded	♀	A	p. April 1973	r.
Unbanded	♂	A	p. April 1973	r.

After group 8 abandoned its territory in February 1973, the area remained unoccupied until April when two birds, both unbanded, moved in. Their history prior to arrival is not known, but it is possible that the male belonged to the previous group. These two individuals remained when the study terminated. They apparently did not attempt to breed in 1973 or 1974.

Group 9

Unbanded	♀	A	p. May 1972	r.
Unbanded	♂	A	p. May 1972	d. June–July 1974
DBLBLG	?	N	b. 16 June 1972	d. June 1972
GWPBl	♂	N	b. 16 June 1972	r.

Group 9 consisted of a pair in the spring of 1972. They bred and fledged two nestlings, one of which soon disappeared. The group, now with three individuals, remained throughout the winter and bred in 1973. They lost two nests, both in the nestling stage. The group remained unchanged until the summer of 1974 when the birds again bred. They lost this nest just before fledging. At about this time the unbanded male disappeared from the group. When the study ended the group consisted of two birds, apparently a mother and her son.

Group 10

GPDB	♀	A	b. 20 Sep. 1972	r.
YPRB	♀	A	b. 19 Sep. 1972	r.
YLB	♂	A	b. 19 Sep. 1972	r.
LPY	♂	A	b. 24 Sep. 1972	d. July–August 1973
LGPLP	♂	A	b. 18 Sep. 1972	r.

Unbanded	♀	A	p. Sep. 1972	r.
Unbanded	♂	A	p. Sep. 1972	r.
DBW	♀	N	b. 26 May 1973	d. winter 1973–74
DPm	♀	N	b. 26 May 1973	r.
LGLG	♂	N	b. 26 May 1973	r.
Om	♂	N	b. 26 May 1973	r.
PDG	♂	N	b. 26 May 1973	r.

Observations began on this group in September 1972. It consisted of four males and three females. The following summer the group fledged five young. The group then consisted of 12 individuals, but one juvenile disappeared during the 1973–74 winter and one adult disappeared during the summer of 1973. This group did not breed in 1974.

Group 11

Unbanded	♀	A	p. March 1974	r.
Unbanded	♂	A	p. March 1974	r.
Unbanded	?	J	f. June 1974	r.
Unbanded	?	J	f. June 1974	r.

This group was not watched intensively although birds were at this location throughout the study. In the spring of 1974 the group consisted of a pair. They bred and fledged two young.

Group 12 (to August 1972)

GLGGLG	?	N	b. 9 June 1972	r.
LGLG	?	N	b. 9 June 1972	d. June 1972
LBW	♂	N	b. 9 June 1972	r.
GBlGBl	♂	N	b. 9 June 1972	r.

Plus unknown number of adults

This group bred in the summer of 1972 and the four nestlings were banded. All fledged but one soon disappeared. The adults were not banded, and it was not possible to census them accurately. In late August 1972, the three banded juveniles and a number of unbanded adults plus two females from group 7 moved to School Hill and occupied part of the territory previously held by group 15. Presumably all of group 12 moved to this area. The move was prompted by acorn crop failure at home.

Group 12 and group 7 (winter of 1972–73)

GLGGLG	(see above)			d. August 1972
LBW	(see above)			m. to group 7a in April 1973
GBlGBl	(see above)			r.
DPLP	♂	A	b. 20 Sep. 1972	r.
YY	♂	A	b. 14 Oct. 1972	r.
YLGR	♂	A	b. 16 Sep. 1972	d. Oct. 1972
Unbanded	♀	A	p. Sep. 1972	r.
Unbanded	♂	A	p. Sep. 1972	r.

WW	♀	A	b. 22 Jan. 1972 at group 7. Moved to School Hill and joined group 12 in August 1972	m. back to group 7 in March 1973
DBDB	♀	A	b. 28 Dec. 1971 at group 7	m. same as for WW

After this group moved to School Hill, we banded three adult males in September and October and were able to make a group count of six males, three females, and a juvenile of unknown sex that disappeared before molt. A male disappeared in mid-October. The group remained unchanged until all birds moved in March and April 1973. The two females originally from group 7 returned to that group. The remainder, except for one yearling, moved back to group 12's original area, which had remained unoccupied during the winter of 1972–73. The yearling moved to group 7's area after that group abandoned its territory.

Group 12 (spring 1973 to August 1974)

GBlGBl	(see above)			r.
DPLP	(see above)			r.
YY	(see above)			r.
Unbanded ♀	(see above)			r.
Unbanded ♂	(see above)			r.
Unbanded	♂	A	Joined group April 1973	r.
Unbanded	♂	A	Joined group April 1973	r.
LPLBm	♂	N	b. 25 June 1973	r.
DB	♂	N	b. 25 June 1973	r.
OLGDG	♂	N	b. 25 June 1973	r.
mPY	?	N	b. 22 May 1974	d. June 1974
LPDPM	?	N	b. 22 May 1974	r.
GGDG	?	N	b. 22 May 1974	r.

Censuses in the spring of 1973 indicated that at least two unbanded males joined the group soon after it moved from School Hill to its own area. The group composition was six males and one female. The group bred and fledged three young. Group composition remained the same through the next year when it fledged three young in 1974. One of these juveniles disappeared in June 1974. The group consisted of eight males, two females, and two unsexed juveniles when the study was terminated.

Group 13

Unbanded	♂	A	p. March–April 1973	d. March 1974
Unbanded	♀	A	p. March–April 1973	r.
GRLBW	♂	A	b. 22 Sep. 1972 at group 16. Moved to group 13 in March–April 1973	r.

During the autumn and winter of 1972–73 group 13's area was unoccupied because of acorn failure resulting from the 1972 freeze. None of the birds that lived here previously had been banded. The area was reoccupied in late March or early April 1973 by three individuals. One of these birds had been banded previously at group 16. The prior history of the other two is not known, but they were not members of group 16. Whether or not any of these birds were members of group 13 before the area was abandoned in 1972 is not known. The group did not breed in either 1973 or 1974.

GROUP 14

This group was not banded and no censuses were made. During most of the study it consisted of at least four individuals. They were affected by the 1972 freeze and abandoned their territory in the late summer of 1972. The area remained vacant until the spring of 1973 when it was reoccupied. It was continuously occupied for the remainder of the study.

GROUP 15

BW	♀	A	b. 11 Feb. 1972	d. August 1972
PLP	♀	A	b. 11 Feb. 1972	d. August 1972. Seen twice in Sep. 1973 but not as a member of a group
BO	♂	A	b. 11 Feb. 1972	d. March 1972
Unbanded	♂	A	p. Feb. 1972	d. August 1972
Unbanded	♀	A	p. Feb. 1972	d. August 1972
GRGR	?	N	b. 4 June 1972	d. August 1972
BlPBlP	?	N	b. 4 June 1972	d. August 1972
BG	?	N	b. 4 June 1972	d. August 1972
BYBY	?	N	b. 4 June 1972	d. August 1972

Group 15 consisted of five birds in February 1972. One male disappeared in March 1972. The group bred in 1972 and fledged four young, all of which survived. The group was displaced from its territory by the combined invasion of groups 4, 7, 12, and birds of unknown origin. Where group 15 went is not known, but in September 1973 one of its members was seen.

GROUP 15a

OBW	♂	A	b. 18 Sep. 1972	d. Nov. 1972
OBYR	♀	A	b. 9 Sep. 1972	d. Nov. 1972
Unbanded	♂	A	p. Sep. 1972	d. Nov. 1972

These birds moved to School Hill in late August or early September 1972 and occupied a part of group 15's old area. Group 15a maintained a territory there until November 1972 when it abandoned the area. The group's history prior to arrival on School Hill and its fate after leaving are unknown. The birds probably moved to this area because of the 1972 acorn crop failure. They did not store because they occupied a part of School Hill that did not have storage trees. They remained there only as long as acorns were present on the oaks.

GROUP 15b

DBPDB	♂	A	b. 6 Sep. 1972	d. Nov. 1972
BWDBR	♂	J	b. 6 Sep. 1972	d. Nov. 1972
Unbanded	♀	A	p. Sep. 1972	d. Nov. 1972

Group 15b consisted of three individuals, one of which was a first-year bird. The birds moved to School Hill in late August or early September 1972 and occupied a part of group 15's old territory. Their history prior to this is unknown. They did not store because the part of School Hill that they occupied had no granaries. They disappeared after the acorn crop was depleted. Their subsequent fate is unknown. Their movement to School Hill was undoubtedly prompted by the acorn crop failure that stimulated so many other groups to move in 1972.

GROUP 15c

Unbanded	♀	A	p. March 1974	r.
Unbanded	♂	A	p. March 1974	r.
Unbanded	♂	A	p. March 1974	r.
Unbanded	♂	A	p. March 1974	r.
RGY	?	N	b. 18 May 1974	r.
MP	?	N	b. 21 June 1974	r.
DGDG	?	N	b. 21 June 1974	r.
mLG	?	N	b. 21 June 1974	r.

Group 15c immediately occupied the area of School Hill vacated by group 12 in March–April 1973. These birds, with the exception of WW (see groups 7 and 12), were all unbanded. Their prior history is unknown. The group was not watched intensively in 1973, but WW appeared to be a member. She left the group in September 1973. Group 15c annexed the territory of group 4 when it left School Hill in the summer of 1973. Group 15c apparently did not begin a nest in 1973. In March 1974 the group was first censused and contained three males and one female. They bred in 1974 and fledged young from two nests.

GROUP 16

BrOO	♀	A	b. 25 Sep. 1972	d. March 1973
GYRY	♀	A	b. 22 Sep. 1972	d. March 1973
GRLBW	♂	A	b. 22 Sep. 1972	m. to group 13 in March 1973

In August 1972 this group occupied an area that had not been occupied by Acorn Woodpeckers since the beginning of the study. The area had once been used by Acorn Woodpeckers, a fact attested to by the presence of several rather derelict granaries. Group 16 undoubtedly moved to this area because of acorn crop failure in 1972. This group stored in one of the old granaries. It left in March but the fate of only one bird is known. GRLBW moved to group 13. Group 16's area was not occupied again during the study.

Group 17

Only one bird (YGLPLB female, banded 5 November 1972) was banded in this group. She remained when the study terminated. We were never able to make a satisfactory count on this group, but at one time it contained at least two other adult females and three adult males. The group apparently did not breed in either 1973 or 1974; certainly no young were fledged in those years, but observations were not extensive enough to determine if the group began nests in those years.

Group 18

LBWRW	♀	A	b. 16 July 1972	d. June–July 1973
PDBPDB	♀	A	b. 16 July 1972	r.
BGO	♂	J	b. 16 July 1972	d. Oct. 1972–March 1973
YDGYDG	♂	A	b. 16 July 1972	d. Oct. 1972–March 1973
RYRY	♀	J	b. 16 July 1972	d. March–June 1973
Unbanded	♂	A	p. July 1972	r.
YW	♂	A	b. 4 Sep. 1972 at group 24. Moved to group 18 in March 1973	r.
WBlW	♂	N	b. 13 June 1972 at group 24. Moved to group 18 in March 1973	r.
Unbanded	?	J	f. June 1974	r.

Five of the six birds in this group were banded in July 1972. The group at this time numbered two adult females, two adult males, and two juveniles probably fledged in the group. Group 18 remained unchanged through October 1972. Two of the birds disappeared between then and March 1973. In March two birds from group 24 joined group 18. After they joined, the group contained three males and three females. One of the females disappeared between March and July 1973, and another, an adult female, disappeared in the summer of 1973. The group then consisted of three males and one female. The group did not breed in 1973. In 1974 it fledged at least one young.

Group 19

OBrOBr	♂	A	b. 24 July 1972	r.
ROY	♀	A	b. 22 July 1972	r.
PYLB	♀	J	b. 23 July 1972	d. Aug.–Oct. 1972
OLBOLB	♀	J	b. 20 July 1972	r.
GYGY	♂	A	b. 19 July 1972	r.
OYOY	♀	J	b. 20 July 1972	r.
Unbanded	♂	A	p. July 1972	r.
Unbanded	♀	A	p. July 1972	r.

In July 1972 the group consisted of eight birds, of which three were juveniles probably fledged in the group. One of the juveniles vanished between August and October 1972.

No other changes in group composition occurred. The group began nests in both 1973 and 1974 but both failed in the nestling stage. During the spring of 1974, OLBOLB and OYOY apparently joined group 21, but they retained ties with their old group and frequented both. They ceased frequenting group 21 by midsummer 1974 and returned permanently to their own group.

GROUP 20

RLBRLB	♀	A	b. 17 July 1972	d. July 1974
LBHPO	♂	A	b. 24 July 1972	d. July 1974

This group contained more than a pair in June 1972, but for unknown reasons, all disappeared except the two listed above. They did not breed in 1973 or 1974 and vacated the area in the summer of 1974. Abandonment may have been stimulated by the collapse of their storage tree. When the group was first observed in 1972 it had one large storage tree that contained several thousand holes. In midsummer 1972, part of the tree collapsed and the group lost about half of its storage space. In the summer of 1973 another section of the tree collapsed leaving very few storage holes.

GROUP 21

OLBm	♂	N	b. 2 June 1972	r.
PWPW	♂	N	b. 2 June 1972	r.
DPDP	♂	N	b. 2 June 1972	r.
O	?	N	b. 9 June 1973	d. Sep. 1973
YLPDBBl	♂	A	b. 28 June 1973	r.
OBrm	♀	A	b. 4 July 1973	d. winter 1973–74
LGLB	♂	A	b. 25 June 1973	r.
DBm	♂	A	b. 23 June 1973	r.
Unbanded	♀	A	p. June 1973	r.
Unbanded	♂	A	p. June 1973	r.
Unbanded	♂	A	p. June 1973	r.

In June 1972 the three nestlings in this group were banded. The following summer the group's single nestling was banded. During June and July 1973 several adults were banded. The group at this time consisted of eleven birds: eight adult males, two adult females, and one juvenile. The 1973 nestling disappeared in September 1973, and OBrm disappeared during the 1973–74 winter. Two birds from group 19 joined this group in the spring of 1974 but did not remain. The group apparently did not breed in 1974.

GROUP 22

PWm	♂	A	b. 20 June 1972	r.
RBY	♂	A	b. 20 June 1972	r.
OM	♂	J	b. 20 June 1972	r.
DBLBLG	♂	J	b. 20 June 1972	r.
LGWPBl	♀	J	b. 20 June 1972	d. spring 1974
GPGP	♂	A	b. 23 July 1972	d. summer 1973
WBW	♂	A	p. July 1972, b. 24 May 1973	r.

DGLGLBW	♀	A	b. 12 August 1972	r.
YDB	♀	A	b. 14 July 1972	r.
Unbanded	♀	A	p. July 1972	r.
Unbanded	♀	A	p. July 1972	r.
Unbanded	♂	A	p. July 1972	r.
Unbanded	?	J	f. June 1974	r.
Unbanded	?	J	f. June 1974	r.
Unbanded	?	J	f. June 1974	r.

Most individuals in this group were banded in the summer of 1972. It consisted of seven males and five females. At least three of the individuals were juveniles presumably fledged in the group in 1972. In 1973 the group began two nests but both failed. In April 1973 the group expanded its territory and took over part of group 23's territory. The part taken contained one of that group's storage trees and one of its sap trees. In July or August of the same year group 22 again expanded at group 23's expense and forced it out of its other storage tree. Group 23 moved to a peripheral section of its territory. Group 22 bred in 1974 and fledged three young.

Group 23

OBm	♀	A	b. 24 June 1972	d. autumn 1973
BWm	♂	A	b. 24 June 1972	d. Sep.–Oct. 1972
LBDB	♀	A	b. 24 June 1972	d. autumn 1973
PLBDP	♀	J	b. 19 July 1972	d. winter 1973–74
RBP	♂	A	b. 14 July 1972	d. summer 1974
OGR	♀	J	b. 14 July 1972	d. April 1973
Unbanded	♂	A	p. July 1972	d. autumn 1973
mBrHP	?	N	b. 11 June 1973	d. summer 1973
YDGM	?	N	b. 11 June 1973	d. summer 1973

In June and July of 1972 group 23 consisted of seven birds, two of which were female juveniles probably fledged in the group that summer. One bird disappeared in September or October and another the following spring. The group lost a nest in midsummer 1972. During April 1973, the neighboring group (22) took over part of group 23's territory. The boundary stabilized and group 23 bred and fledged two nestlings that year. Both disappeared that summer. In late July or early August, group 22 again expanded its territory and took over most of the remainder of group 23's territory. Group 23 moved to a small part of its territory but most individuals disappeared shortly thereafter. Only two individuals remained in the area and stored in desiccation cracks. The female disappeared during the winter. When we surveyed the group in the spring of 1974, two birds, RBP and an unbanded female, obviously from elsewhere, occupied the area. They remained together in this area until midsummer when they abandoned it.

Group 24

WO	?	N	b. 13 June 1972	d. June 1972
DGR	♀	N	b. 13 June 1972	d. autumn 1973–spring 1974
WBlW	♂	N	b. 13 June 1972	m. to group 18, March 1973

DBLBOG	♀	A	b. 26 August 1972	d. autumn 1973–spring 1974
W	♂	A	b. 24 August 1972	r.
YOLG	♀	A	p. August 1972, b. 28 March 1973	r.
RW	♂	A	p. August 1972, b. 26 March 1973	r.
YW	♂	A	b. 4 Sep. 1972	m. to group 18, March 1973
PWLBR	♀	A	b. 3 Sep. 1972	d. Aug.–Sep. 1973
Unbanded	♀	A	p. August 1972	r.
Unbanded	♂	A	p. August 1972	r.
Unbanded	♀	A	p. August 1972	d. autumn 1973–spring 1974
GLGO	?	N	b. 4 June 1973	d. July 1973
LPYDP	?	N	b. 4 June 1973	d. autumn 1973–spring 1974
LBRDB	?	N	b. 4 June 1973	d. autumn 1973–spring 1974
mPDB	♂	N	b. 4 June 1973	d. autumn 1973–spring 1974
BrHPm	♀	N	b. 4 June 1973	d. autumn 1973–spring 1974
LBWm	?	N	b. 4 June 1973	d. July 1973

The leucistic male (W) observed in this group in 1968 was still present in the group when the study terminated and was thus at least 6 years old. The first birds banded in this group were three nestlings in 1972. Enough adults were banded in August and September to allow an accurate group count. The group numbered eleven individuals during the winter of 1972–73. In March two of the males moved to group 18. The group bred in 1973 and fledged six young. This was the largest number fledged by any group from one nest during the study. Two of the juveniles disappeared in July. In June 1973 the group numbered 15 individuals. Between autumn and spring 1973–74 most of the group disappeared. The 1973 acorn crop was poor, and it is probable that group 24 ran short of food sometime in late winter or early spring. Five members remained in the spring of 1974. They did not breed that year.

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