

# ACORN WOODPECKER BREEDING STRATEGY AS AFFECTED BY STARLING NEST-HOLE COMPETITION

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The aggressive, skillful tactics used by the introduced Starling (*Sturnus vulgaris*) in acquiring nest-holes have been extensively documented by Kalmbach and Gabrielson (1921), Howell (1943), Bent (1950), and others (see below and Troetschler 1970), but it is not known whether the Starling is detrimental to the breeding success of any native North American bird. The present study was designed to determine if competition with Starlings for tree holes is changing the breeding strategy and/or lowering the fecundity of the Acorn Woodpecker (*Melanerpes formicivorus*) in California.

The Acorn Woodpecker is a unique, social species resident in the oak belt of western North, Central and South America. Individuals live and breed cooperatively, defend stores of acorns (each acorn tightly fitted into a woodpecker-made socket) and collectively defend a year-round territory which includes the nest tree(s), storage tree(s), and oaks which supply the mast (Myers 1923, Leach 1925, Ritter 1938, Skutch 1943, 1961, 1969, MacRoberts 1970, MacRoberts and MacRoberts 1972). It seems possible that this species has an advantage over other competitors for Starling holes such as bluebirds, flycatchers or other woodpeckers because its social groups may permit better defense and more rapid construction of holes. Alternatively, however, its resident nature may limit flexibility in choice of nesting sites.

## POTENTIAL IMPACT OF THE STARLING

Natural or experimental modifications of an environment can result in temporary or permanent changes in population size or structure of its inhabitants. Thus, if nest-holes are limiting to hole-nesting birds (Brown 1969), as von Haartman (1956) concluded for the Pied Flycatcher (*Ficedula hypoleuca*), and Laskey (1940) for the Eastern Bluebird (*Sialia sialis*), then the exponential increase in the North American Starling population (Davis 1950, DeHaven 1973) may have been accompanied by the displacement of a comparable number of hole-nesting pairs of other species, with a corresponding decrease in their reproductive success. However, the populations of these native species would de-

cline only if the numbers of their mature offspring were less than the populations of the parents when averaged over a period of years (Nicholson 1957).

## EVIDENCE OF PREVIOUS STARLING IMPACT

Kalmbach and Gabrielson (1921) found no evidence of population decline in seven hole-nesting species which had been sympatric with Starlings for 15 years. They presented no population data to support their conclusions, however. In California, Plank (1967) found little competition for nest boxes but did observe that Starlings preferred natural sites. He found that as his study progressed, an increasing number of native species and individuals used the boxes. Starling acceptance of boxes did not increase. Plank's observations may have indicated native birds transferring to the boxes after natural sites were taken by Starlings. Myres (1958) observed that Starling nesting increased sixfold during three years in British Columbia, but at least initially, unused holes were available for Starling use. Kilham (1958a, 1969) noted species differences in the response of woodpeckers to Starling hole competition. A Red-bellied Woodpecker (*Centurus carolinus*) pair failed to breed, but Hairy Woodpeckers (*Dendrocopos villosus*) fledged offspring late in the season after losing an earlier hole to Starlings. Kilham (1958b) further reported that eight Red-bellied Woodpeckers lost roost holes in winter, but that no roost holes were lost by Red-headed Woodpeckers (*Melanerpes erythrocephalus*), a more social species than the other picids just noted.

From data on number of pairs breeding in Trelease Woods, Urbana, Illinois (Kendeigh 1944, Breeding Bird Census 1944-1945, 1946-1970, 1971-1973), I analyzed information on the Yellow-shafted Flicker (*Colaptes auratus auratus*), the Red-headed Woodpecker, and the Starling, potentially competing forest-edge species. The initial period for which data are available, 1929-1954, was stable, and the Trelease Woods environment remained unchanged. Trend lines (Simpson et al. 1960) for these years show the count of breeding pairs of the two woodpeckers remained stable, while the Starling population increased sig-

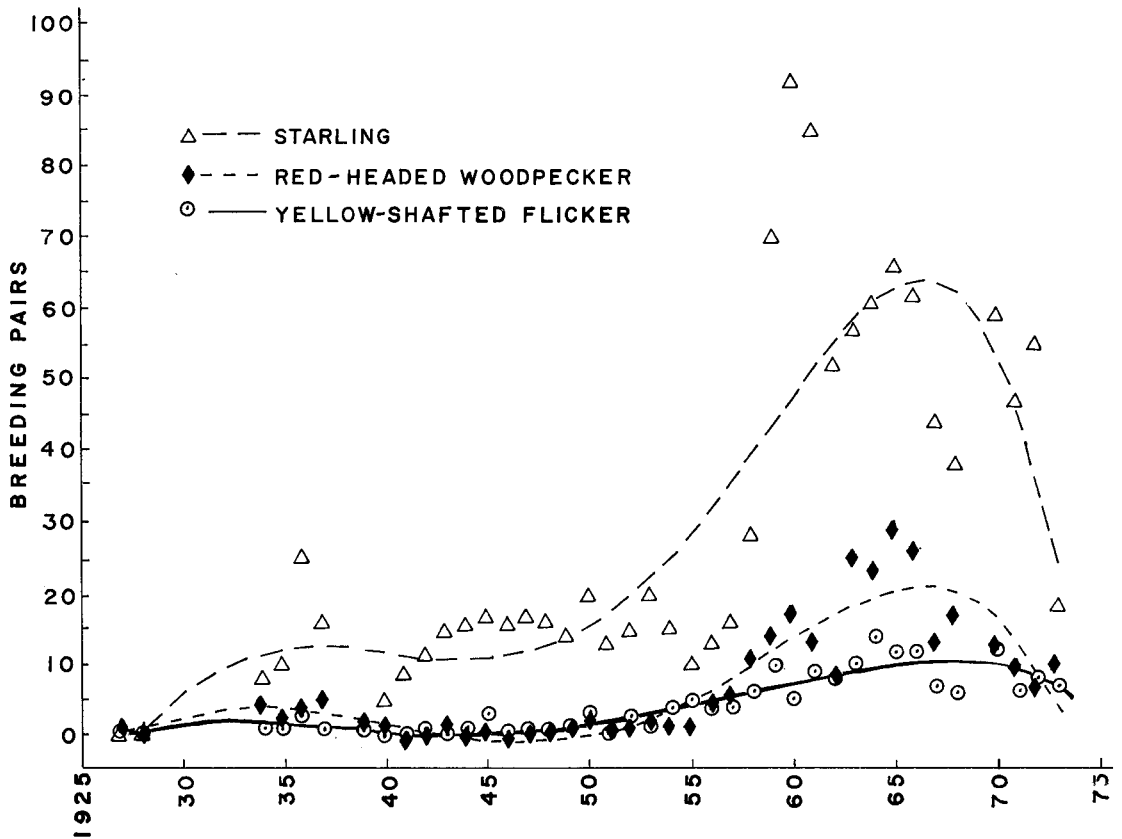


FIGURE 1. The number of pairs of Starlings, Red-headed Woodpeckers, and Yellow-shafted Flickers breeding in Trelease Woods, Urbana, Illinois from 1925-73. Environmental changes occurred after 1955 (see text). Curves fitted by a 5-degree polynomial regression using least squares fit (Hewlett Packard 09830-70000 Plotter Pack).

nificantly ( $\alpha \geq .05$ ). Beginning about 1955, when the native elms (*Ulmus americana*) began to die, the available edge increased. Possibly food and number of nest sites for these three species increased as well. Analysis of 1955-1969 data showed a significant increase ( $\alpha \geq .05$ ) in numbers of all three species (Troetschler 1970). Figure 1 shows curves for the entire 46 years fitted by 5-degree polynomial regression using least squares fit (Hewlett-Packard 09830-70000 Plotter Pack). In this woods the presence of Starlings seems not to have caused a decrease in the number of breeding pairs of these two native woodpeckers. However, changes in the environment were accompanied by first an increase and then a decrease in numbers of each.

#### MATERIALS AND METHODS

During the present study in Los Altos and Los Altos Hills, Santa Clara Co., California (fig. 2), from March 1968 through August 1974, I recorded the breeding and interspecific interactions of Starlings and Acorn Woodpeckers in, at any one time, four principal and several peripheral study areas. Each area included the territory of an Acorn Woodpecker

group and was representative of one of the three local variations of the Oak Savannah. The oaks in the areas were *Quercus lobata* and *Q. agrifolia*. In Clustered Oak Savannah (Byrne Park, Elena, Taafe), each group of woodpeckers defended a cluster of massive oaks surrounded by grassland. Scattered Oak Savannah featured grassland with evenly-spaced, but rather small oaks. The territories in this sub-habitat (Poplars, Ride School) were larger, with less defined boundaries. Ritter (1938) described similar Acorn Woodpecker use of Oak Savannah. Disturbed Oak Savannah areas were urban (Los Altos Supply) and suburban (Los Altos, Foothill) in character. These several sites, all within an area 6.4 km in diameter, varied in elevation from 24 to 180 m.

Observations were made primarily in the morning, one to five times bi-weekly throughout the year for a total of 785 hr (fewer visits in winter than in other seasons). Six-power binoculars and a 15-60 power zoom scope enabled long distance recognition of details. Many observations were made from a blind. Behavioral interactions were noted as they occurred with time recorded at 2 to 5 min intervals. Although no birds were color-marked, Acorn Woodpeckers in five study areas (Byrne Park, Foothill, Los Altos Supply, Elena, Ride School) were recognized individually and their individual behaviors recorded. Figure 3 is an example of sketches used as aids in identification.

In the San Francisco Bay Area, Starlings breed in

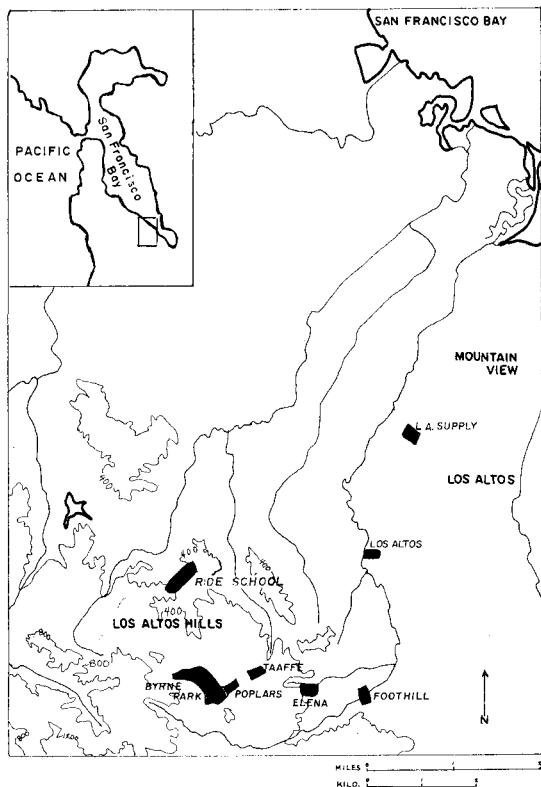


FIGURE 2. Location of the study areas in the communities of Los Altos and Los Altos Hills, California.

woodpecker holes, in natural tree cavities, in holes in buildings and in the skirts of Washington Palms (*Washingtonia filifera*). My study was confined to records of cavity-nesting Starlings. Because it is difficult and dangerous to obtain data from holes located 11 to 31 m up and often in rotten trees or limbs, I made no attempt to count eggs or nestlings of either species. Egg dates were estimated from hatching and fledging dates and from observations of parental behavior and developmental parameters of the nestlings (table 1), e.g., the parents entering to feed, loudness of the voices of the young, extent of oral flange. A nest from which at least one young flew (Collins and de Vos 1966) was considered successful.

All data were combined and analyzed as observations per hour grouped in 15-day intervals. Then data from the first three years were compared with those from the second three years to determine if changes in behavior and other parameters of breeding

TABLE 1. Developmental parameters used to estimate egg dates, hatching dates, and ages of juvenile Acorn Woodpeckers and Starlings (Lawrence 1966, Royall 1966).

	Approximate number of days parameter observed (begins after hatching)									
	Egg Laying	Incub. eggs	Inside <sup>a</sup> feed	Quiet voices	Corridor <sup>a</sup> feed	Top <sup>a</sup> feed	Oral flange	Fledg. feed	Fledg. <sup>a</sup> molt	Eyes dark
AWP <sup>b</sup>	4(-18)	14(-14)	11(0)	—	10(11)	7(21)	33(0)	25(28)	30-60(58)	58(0)
S <sup>b</sup>	4(-16)	12(-12)	8(0)	5(0)	6(8)	6(14)	19(0)	1(20)	—	—

<sup>a</sup> Inside feed = parent enters hole to feed. Corridor feed = parents tip up to feed young clinging out of sight near the top. Top feed = parents feed young which are visible at the top. Fledging molt = all juveniles resemble adult males until this partial molt.

<sup>b</sup> AWP = Acorn Woodpecker, S = Starling.

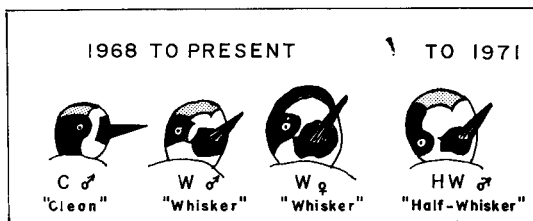


FIGURE 3. The Acorn Woodpeckers of Byrne Park study area (1968-74). Illustrations are based on field sketches and include facial characteristics used in individual identification. Letter names stand for phrases describing these identifying characteristics.

success had occurred. Naturally, all conclusions must be considered tentative. Short-term climatic variations may have influenced reproductive success so as to obscure effects of Starling competition which may become evident only over a longer time span.

RESULTS

PATTERN OF STARLING VISITATION

The Starlings observed were primarily a resident group which followed a sequence of hole-orientated activities in the nonbreeding season (Bullough 1942, Kessel 1957). *S. vulgaris* first bred in the Los Altos area between 1965 and 1969. Thus by the time the study began at least a few Starlings were visiting most Acorn Woodpecker territories almost every morning and evening throughout the year (Troetschler 1970). A single classification analysis of variance (anova; Sokal and Rohlf 1969) showed that the pattern of morning visitation, measured as mean number of Starlings arriving per observation hour, did not differ significantly from year to year (fig. 4A). Peaks of visitation occurred in late January when resident male Starlings begin to establish territories (Bullough 1942, Kessel 1957), in spring, before, during and after breeding, and in fall during Starling migration. Although 90% of the Starling visitors stayed only 5 to 10 min, during peak seasons they were present 85% of the time (Troetschler 1970).

The Starling visitors sang and often approached the holes (fig. 4B). Many such

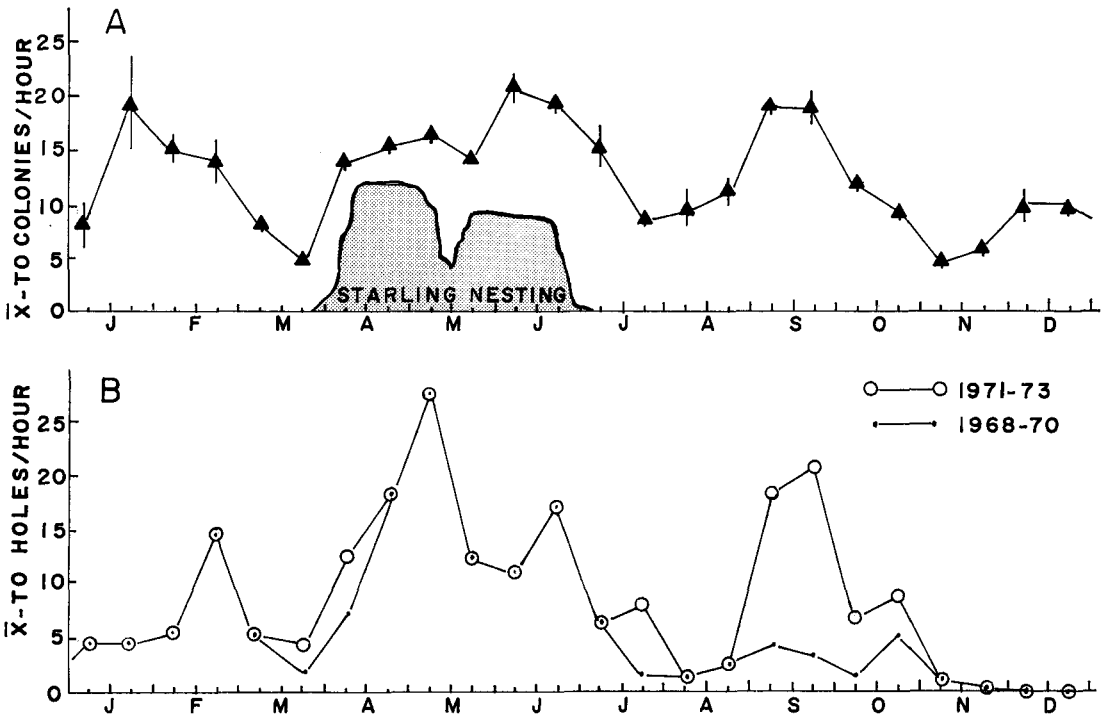


FIGURE 4. Annual pattern of Starling activities in Acorn Woodpecker colonies (1968-73). A. Mean number of Starlings arriving per observation-hour. Vertical lines represent 95% confidence limits. Starling nesting: mean number of pairs nesting. B. Mean number of Starlings approaching holes per observation-hour. Where significant differences ( $P \leq .001$ ) were observed between seasons, a double curve is presented.

hole visits may have been only exploratory, however, since hole visitation peaks did not always correspond to the major periods when the woodpeckers lost holes. Acorn Woodpeckers usually responded to hole losses in January, February, and early March by excavating another hole. In some instances the new hole was lost in April or early May during the spring peak of Starling hole visitation. This peak occurred near the end of the Starling's first breeding period (fig. 4). Starlings approaching holes at this time included parents feeding young and large numbers of non-breeders which rather suddenly began to visit (1) old, marginal, but empty holes; (2) new Acorn Woodpecker holes; (3) holes containing Starling nestlings a few days from fledging. These visiting strangers helped to increase the mean number of territory visits by different individuals to over 15 per observation hour (fig. 4A). A few non-breeding Starlings investigated holes throughout the nesting period, but this sudden increase requires a different explanation. Perhaps these birds represented early breeders searching for holes for the second brood, or, alternately, they may have been migrants and/or yearlings reaching

breeding condition later in the season than more mature and/or resident birds.

As the second *S. vulgaris* breeding season began, fewer Starlings visited holes, but later, parents feeding young increased the hole-visit count. At the same time non-breeding Starlings coming to the territories (but not the holes) increased to a mean of over 20 visitors per observation-hour. Fewer Starlings bred during the second period, but many non-breeding adults and juveniles visited through June and early July. During the second breeding, the locations of Starling nests were discontinuous. In the drier territories, few Starlings reared a second brood, but in moist areas, more holes, including marginal holes, were used for breeding. *S. vulgaris* broods nestlings for only a few days (Kessel 1957). In the cool early spring only the better holes are adequate for nestling protection. Later, as the weather warms, old holes with large worn entrances are used in those moist sub-habitats that still can supply adequate nestling food. These variations in use of holes by Starlings may be important to the woodpeckers in that they free holes and reduce Starling visits earlier in some areas than in others.

TABLE 2. Status of holes at Byrne Park (BP), Elena (EL), and Foothill (FH) study areas.

	Holes (destroyed) <sup>a</sup>				Holes used by Starlings			
	BP	EL	FH	Total	BP	EL	FH	Total
1968	2	2	3	7	1	0	2 <sup>b</sup>	3 <sup>b</sup>
1969	3	5	6	14	3	4	5	12
1970	4	8	7	19	4	2	7	13
1971	4	9	8(2)	21(2)	4	3	7	14
1972	5	5(3)	9	19(3)	5	1	8	14
1973	6	6	10	22	6	1	9	16

<sup>a</sup> Tree fell or was removed.<sup>b</sup> Estimated.

During the first three years, Starlings showed little summer interest in Acorn Woodpecker holes, although large numbers of adults and juveniles visited them in the fall. During the second three years, however, Starling hole visits increased significantly in July (anova,  $P \leq .05$ ) and again in September and October ( $P \leq .001$ ). Thus, Acorn Woodpeckers were exposed to more Starling hole visitors over a longer period than at the beginning of the study.

#### S. VULGARIS HOLE-COMPETITION STRATEGY

Between June and October, whenever a Starling visits an "Acorn Woodpecker hole" (one in current use), Acorn Woodpeckers often respond with attack, but in January, February, and early March, when most holes are lost, the woodpeckers usually continue other activities without obvious response. *S. vulgaris* usually attacks only conspecific hole owners. A Starling may wait in the area until the woodpecker residents leave the nest tree, then quickly approach the hole. If the owners do not return, it may enter. If it is evening, the Starling may remain in the hole overnight (M. M. Erickson, pers. comm.). As the breeding season approaches, the Starling may attempt to stuff nesting material into the cavity.

Usually by that time almost any hole is already a "Starling hole," i.e., one the woodpeckers have failed to defend during a two-week period. However, the woodpeckers continue to attack non-breeding Starling visitors who approach nest trees all through the Starling breeding season.

I seldom have seen *S. vulgaris* attack an Acorn Woodpecker or any other heterospecifics. The few attacks that occurred were counterattacks. However, if a woodpecker flies to a different tree, a Starling usually follows. If a woodpecker begins a new hole, a Starling watches. During the fall, all cavities are investigated by both adult and juvenile Starlings.

*S. vulgaris* has proved a formidable competitor for Acorn Woodpecker holes. Table 2 reflects the proliferation of holes in the three areas where they have been monitored over the entire six years. In these territories, the total number of nest-holes increased 64%, and the Starlings breeding there increased 81%. In addition many holes were used by Starlings twice each year. In some territories entire trees containing 3 to 7 holes were abandoned by woodpeckers to exclusive Starling use. *S. vulgaris* reproduction in these and other holes is summarized in table 3.

The variation in Starling fecundity and egg dates may be due to weather variations. In years with a cold spring, e.g., 1969, 1971, and 1973, nest success was better in the second cycle. In hot, dry 1970, success was better in the first cycle. The most successful year, 1968, had warm, mild weather throughout the spring season. Success was not monitored in 1973.

#### PATTERNS OF *S. VULGARIS* HOLE USE

Starling use of available cavities (table 2) varied considerably. After 1968, every hole at Byrne Park was used twice each year, at

TABLE 3. Parameters of Starling reproduction, 1968-73, at principal study sites.<sup>a</sup>

	Egg Dates <sup>b</sup>				% Success <sup>c</sup>		Hole-Nests Monitored
	1st Brood		2nd Brood		1st Brood	2nd Brood	
	$\bar{x}$	Range	$\bar{x}$	Range			
1968	4/5	4/2-4/10	5/17	5/12-5/20	85	87	15
1969	4/6	4/2-4/12	5/20	5/16-5/22	58	77	21
1970	3/31	3/27-4/12	5/18	5/14-5/20	71	54	18
1971	4/9	3/29-4/22	5/23	5/18-5/28	67	80	24
1972	3/31	3/25-4/13	5/19	5/8-6/13	—	—	9
1973	4/7	3/25-4/22	5/19	5/8-6/13	78	73	24

<sup>a</sup> To compare with other U.S. Starling breeding records see DeHaven and Guarino (1970).<sup>b</sup> Intermediate nests not included.<sup>c</sup> Intermediate nests recorded in second cycle.

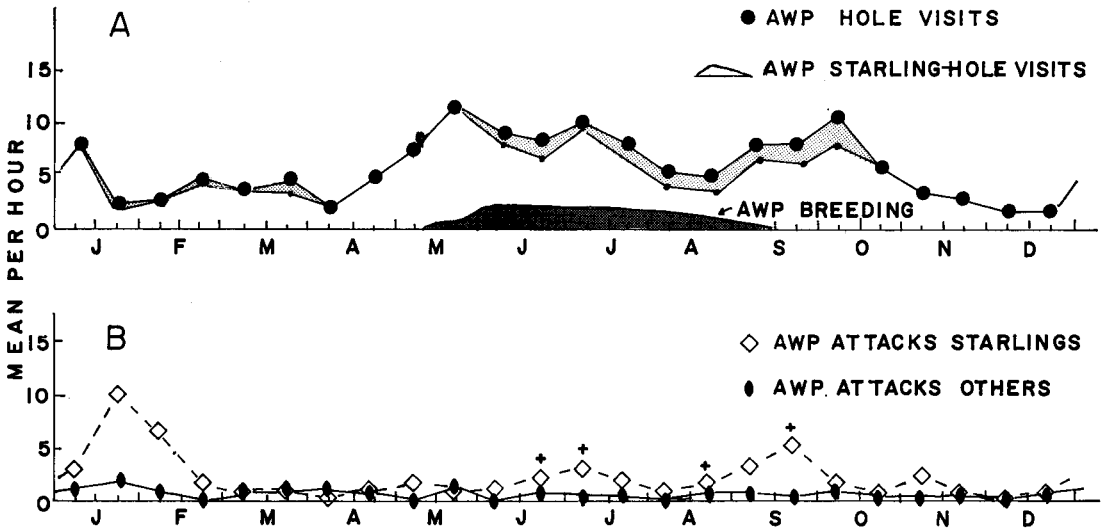


FIGURE 5. Acorn Woodpecker (AWP) activities 1968-74. A. Mean number of hole visits per observation-hour. AWP breeding: mean number of Acorn Woodpeckers breeding. B. Mean number of attacks on heterospecies per observation-hour. + indicates significantly greater number of attacks on Starlings ( $P \leq .05$ ). Most 95% confidence limits,  $\bar{x} \leq \pm 4.4$ ; Jan. 16-31 =  $\bar{x} \pm 28$ , Feb. 1-15 =  $\bar{x} \pm 13$ .

Elena many were unused, and at Foothill, use was intermediate. However, the number of holes retained by the woodpeckers seemed not to determine their breeding success (see below). In 1968, one pair of Western Bluebirds (*Sialia mexicana*) bred in an old Acorn Woodpecker hole. In 1969 this pair (?) failed to breed when no suitable cavity was available upon their return from migration. A pair of Ash-throated Flycatchers (*Myiarchus cinerascens*) briefly attacked Starlings with nestlings at Byrne Park. The flycatchers later bred successfully in a natural cavity. I have seen no other native hole-nesting species attempting to use Acorn Woodpecker or Starling holes, although House Sparrows (*Passer domesticus*) were excluded from all but crevice-holes at Los Altos Supply.

#### ACORN WOODPECKER RESPONSE TO STARLINGS

Acorn Woodpeckers may respond to Starlings presence with vocalizations and displays. The *jacob* call (Myers 1923), although primarily an intraspecific call, is sometimes heard in relation to Starlings. The woodpeckers may *jacob* at the approach of a flock of Starlings or immediately after Starlings depart following a period of intense conflict. The general alarm call, *ka-ra-ah* (Myers 1923), *kr-ra-ka* (Grinnell and Storer 1924), *karrit-cut* (MacRoberts 1970), is heard repeatedly as a reaction to *S. vulgaris*. Group-members respond to this call first by looking, and then possibly by flying toward the calling woodpecker. The *ka-ra-ah*

may be repeated up to 25 times when a Starling is inside an Acorn Woodpecker hole. This call is used in all alarming situations, and *S. vulgaris* responds appropriately, e.g., Starlings fly toward the calling woodpecker during hole conflict, but drop suddenly into dense vegetation after the call is given in the presence of a hawk.

An Acorn Woodpecker may threaten by pointing its bill directly at a Starling, or may supplant it by hitching up the tree beneath its perch, forcing it to fly. Such displacement is often followed by aerial attack (the "supplanting" of MacRoberts 1970). During attack, the woodpecker flies directly toward the offending bird, even striking it at times. An attack by one Acorn Woodpecker frequently is followed immediately by the attack of another woodpecker on the same, or other nearby Starling. Similarly, once an attack is launched, a single woodpecker may attack the same or another Starling several times in rapid succession. An attacked Starling may leave the territory but more often remains somewhere nearby.

Figure 5A illustrates the mean number of Acorn Woodpecker attacks on all species per observation-hour, during the six year study. A plus denotes a season when the woodpeckers attacked individual Starlings significantly more often than individuals of all other species combined (anova,  $P \leq .05$ ). Other than *S. vulgaris*, Acorn Woodpeckers were most likely to attack major food competitors such as jays, squirrels, and nuthatches, though

a large flock of any one species would elicit attack(s). Unlike the groups observed by MacRoberts (1970), these groups did not attack all heterospecifics that landed in acorn storage trees, nest trees, or on hawking perches. On a number of occasions, for example, an Olive-sided Flycatcher (*Nuttallornis borealis*) hawked for insects at such a site for long periods without being disturbed by the woodpeckers. Acorn Woodpeckers also did not attack every Starling that entered such trees. This would have been extremely costly energetically, because a three- or four-member colony was at times confronted with as many as 35 Starlings. However, the greater number of attacks on *S. vulgaris* is indicative of still other behavioral changes that have occurred in the woodpeckers. When Starlings are present, the Acorn Woodpeckers are more likely to remain in the nest tree and more likely to fly to the holes (Troetschler 1970). It is probable that such behavioral changes have an adverse effect on the time-energy budget of the species.

#### ACORN WOODPECKER BREEDING STRATEGY

Acorn Woodpeckers have a strong hole orientation, even more intense than that of the Starlings. Throughout the year they periodically fly to the holes, seemingly as a Check or Recognition Display (see Ritter 1938:43). They express most intense hole interest from May through October (fig. 5B). This long period of hole orientation may be related to their asynchronous breeding season. When I plotted Acorn Woodpecker egg dates in 15-day intervals, I found several nest starts in each interval from 1 May through 15 August. Only in July and August were any of these starts second nestings. The mean egg-date from my data was 1 June. Thus most local Acorn Woodpeckers began to breed in the middle of the Starling breeding season (figs. 4, 5; table 7).

In my experience the following events have resulted in Acorn Woodpecker nest starts: (1) hole not found by Starlings; (2) hole-of-the-year recovered after Starling use; (3) new hole completed during the second Starling breeding; (4) hole successfully defended (once). In the first three years, groups that excavated cavities away from the main acorn storage and/or nest tree(s) usually succeeded in laying eggs and hatching young before Starlings found the site. In the second period, however, Starlings consistently found such scattered holes and used them for breeding. For example, in the 1973-74 winter pe-

TABLE 4A. Parameters of Acorn Woodpecker breeding, 1968-74, at all study areas.

	1968	1969	1970	1971	1972	1973	1974
No. Groups	5	8	8	6	5	6	6
Total Adults	13	22	17	17	13	18	18
Adults Breed- ing	13	14	5	7	8	13	15
Nest Starts	6	6	3	3	4	6	6
Fledged	6	11	4	5	6	7	9
Fledged/ Group	1.3	1.4	0.5	0.8	1.2	1.2	1.5
Successful Nests	2	5	2	3	4	4	5
Fledged/Nest	1.0	1.8	1.3	1.7	1.5	1.2	1.5
Fledged/ Adult	0.4	0.4	0.2	0.3	0.5	0.4	0.5
Groups Breeding	5	6	3	3	3	5	5
% Groups Breeding	100	75	25	50	60	83	73
Adults/Group	2.6	2.7	2.1	2.8	2.6	3.0	3.0
Ad./Brdg. Group <sup>a</sup>	3.6	1.7	2.5	2.3	2.7	3.0	3.0
Ad./Non- Brdg. Group	—	3.8	2.0	3.0	2.5	3.0	3.0

<sup>a</sup> Ad. = Adults; Brdg. = Breeding.

riod the Foothill group excavated and lost three scattered holes before they succeeded in keeping a fourth for their own breeding. Need for such repeated hole digging (even though accomplished rapidly by a group) suggests adverse effects of Starling competition on woodpecker time-energy budgets as well as delay of woodpecker breeding to a less optimum time of year. The lightly shaded area in figure 5A corresponds to the mean frequency at which Acorn Woodpeckers visited Starling holes. The fact that the Acorn Woodpeckers spent so much time in efforts to recover old holes suggests that before the Starlings' advent the woodpeckers commonly reused old holes for roosting and nesting. Both Leach (1925) and Ritter (1938) observed nest-hole reuse. During my study, Acorn Woodpeckers attempted to recover only holes-of-the-year from Starlings for breeding. Other older Starling holes were recovered for roosting.

#### ACORN WOODPECKER FECUNDITY

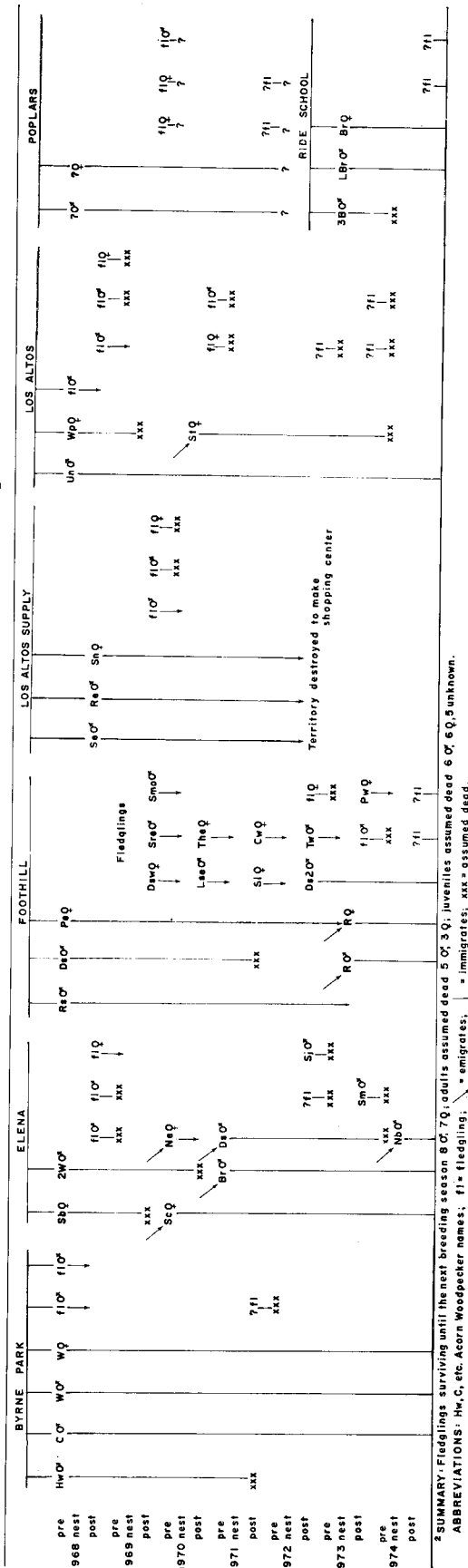
The fecundity of Acorn Woodpecker groups varied greatly, even between those of similar habitats and apparent Starling impact (table 4). In the Byrne Park territory, only one nestling was fledged during the 6-year period, and it survived less than two months. On several occasions a group of woodpeckers made no obvious attempt to breed after initial hole loss. However, the Foothill group fledged

TABLE 4B. Parameters of Acorn Woodpecker breeding at all study areas, summarized for the two three-year periods of observation.

	1968-70	1971-73	Total
Number different groups	8	7	10
Number different adults	22	20	30
Nest starts	15	13	28
Fledglings	20	18	38
Fledglings/group/year	.83	.83	.83
Successful nests	9	11	20
% Success	60	85	71
Fledged/nest	1.2	1.4	1.3
Fledged/adult/year	0.3	0.3	0.3
% Groups breeding/year	54	64	59
Adults/group	2.5	2.8	2.7
Adults/breeding group	2.3	2.7	2.5
Adults/non-breeding group	2.7	3.0	2.9

and successfully maintained until the following spring one to three young in five of the six years. On three occasions groups nested again after successfully fledging young early in the year. In addition, several groups nested again after a first unsuccessful attempt. When data from the first and the second three-year periods were compared, every breeding parameter studied showed almost complete identity. Therefore it was assumed that none of the factors listed (table 4B) differed. Incubation began in 13 nests in each period. From these nests, a mean of 1.3 and 1.4 young were fledged per nest. Groups included two to four adult woodpeckers with only one female per group. The mean colony sizes of breeders were 2.3 and 2.7, and of non-breeders, 2.5 and 2.8. This suggests that the presence of Starlings has neither adversely affected local Acorn Woodpecker fecundity nor altered group size. M. H. MacRoberts (pers. comm.) recently reported a mean of 0.2 fledglings per adult per year during a 6-year study at Hastings Reservation, Monterey Co., California, where Starlings have had minimal impact. Los Altos groups averaged 0.3 fledglings per adult per year. In any one year only about 60% of the groups attempted to breed but during any three-year period every group nested at least once and most nested twice. The reason for this sporadic breeding is not yet apparent. However, 1969, 1973, and 1974, years of many breeding attempts, followed rainy winters. The primary food for nestlings is adult insects which are caught on the wing. It is possible that breeding is closely correlated with the local supply of such insects. The 71% nest success compares favorably with that of other species which have not been stressed by invading species.

TABLE 5. Longevity, reproduction and group structure of Acorn Woodpeckers.<sup>2</sup>



<sup>2</sup> SUMMARY: Fledglings surviving until the next breeding season 6 ♂, 7 ♀, adults assumed dead 5 ♂, 3 ♀, juveniles assumed dead 6 ♂, 6 ♀, 5 unknown. ABBREVIATIONS: Hw, C, etc. Acorn Woodpecker names; fl = fledgling; i = immigrant; xxx = assumed dead.



ACORN WOODPECKER LONGEVITY,  
REPRODUCTION AND GROUP STRUCTURE

Preliminary evidence based on tabulation of the longevity, reproduction, and group structure of the colonies in the principal study areas (table 5) suggests that adult Acorn Woodpeckers are remarkably long-lived. Many of the adults first seen in the spring of 1968 were still alive in the spring of 1974. More than 50% of the fledglings, however, did not survive their first winter even though young birds remained with their parents in a territory containing stored food and roost holes. The parents fed the fledglings for approximately 6 weeks. The young, in turn, participated in acorn storage, hole digging, feeding of later nestlings, and territorial defense. All surviving fledglings disappeared in April or May, and I assumed that they emigrated at that time. Likewise, any increase in colony size occurred in spring. When a female of the Los Altos group was killed by a car in spring, 1969, the two males remained alone on the territory until the following spring when a female joined the group (table 5). Again, when the female disappeared from Elena in winter 1969, no female joined the group until in spring 1970. The following winter the male died, and he was replaced by two new males in spring 1971. Thus, none of the fledglings remained with the parents during the following breeding season, and all new group members were believed to be non-relatives, although the origin of the birds joining the colonies was not known. Throughout the year, but especially in the spring, lone Acorn Woodpeckers appeared on the territories. Usually such birds were immediately driven away by the colony members, but occasionally, even in the presence of another group member of the same sex, the stranger was allowed to join the group. I believe that most of these lone birds are juveniles, although adults also are known to change territories (M. M. Erickson, pers. comm.).

From time to time, major contests occurred in which an invading group of Acorn Woodpeckers tried to take over a territory of another group. On one occasion they succeeded. In spring 1973, almost the entire composition of the Foothill group changed (table 5). Some other reasons for group emigrations can be suggested. The Los Altos Supply group had to emigrate when their territory was destroyed. Michael (1926) described migration of Acorn Woodpeckers of Yosemite Valley after the acorn crop failed. At least some of

TABLE 6. Mortality of Adult Acorn Woodpeckers.

	Number males		Number females		Total
	Observed	Dying	Observed	Dying	
1968	10		6		
1969	9		5	2	
1970	8	1	4		
1971	7	2	3		
1972	8		4		
1973	9	2	6	1	
Total	51	5	28	3	
$\bar{x}$ /yr.	8.5	0.73	4.66	0.5	
$\bar{x}$ /deaths/adult/yr.	0.086		0.109		0.10

them returned the following spring. It would be advantageous for such a group to take over an established territory rather than to pioneer unknown and untested areas (see below).

Skutch (1943, 1945) predicted that the age at first breeding in the Acorn Woodpecker is greater than one year. I have only one observation bearing on this. A young male banded in June 1974 did not have a cloacal protuberance. This bird was an outsider trying to join the Byrne Park colony and may not have been in breeding condition for this reason. As juveniles can be recognized for many months by tone of voice, bill length, and plumage (Troetschler 1974, Spray and MacRoberts 1975), careful observation of new group members should reveal age at first breeding.

I assumed that the disappearance of one Acorn Woodpecker indicated death but that disappearance of a group indicated emigration. Most adults died in winter, indicating that this is a time of stress in spite of stored food and protective roost holes. Juveniles died at least in summer, fall, and winter. Although young birds had an equal sex ratio (all nestlings and very young fledglings look like adult males, but 4 to 8 weeks after fledging, juvenile females can be distinguished; table 1), adult male birds predominated in the groups (table 5). A further analysis of information in table 5 suggests reasons for the unbalanced adult sex ratio. These data show that the death rate for adult males was 0.086 per adult male per year; that for adult females was 0.109 (table 6). At these unequal death rates, it would take only five adult years for the observed sex ratio of 1.64 males to one female to be manifest. These data suggest, furthermore, that the local Acorn Woodpeckers have a life span of about eleven years, with males living about thirteen years and females about ten.

TABLE 7. Acorn Woodpecker Egg Dates.<sup>a</sup>

	Prior to 1941	NRCP	This study
3/1-3/15	1		
3/16-3/30	1	1	
4/1-4/15	3	2	
4/16-4/30	5	2	1
5/1-5/15	1	8	6
5/16-5/30	1	1	7
6/1-6/15	1		6
6/16-6/30	2		2
7/1-7/15			2
7/16-7/30			1
8/1-8/15	2		4
8/16-8/30	3		
9/1-9/15	1		
Mean	5/15	4/22	6/1
$\sigma$ (days)	15	4.4	6.2

<sup>a</sup> Dates of nests from all sources determined as in table 1. Nests with incomplete descriptions were omitted. References for records prior to 1941 cited in Troetschler 1970. NRCP = North American Nest Record Card Program.

#### OTHER FACTORS BEARING ON STARLING COMPETITIVE SUCCESS

I investigated the possibility that hole loss to Starlings caused the Acorn Woodpeckers to breed later in the season than in the past. An analysis of variance of the egg dates from 71 nests showed no significant differences between the mean dates of nests prior to 1941, 15 May, of nests reported by participants in the North American Nest Record-Card Program (1965-1973), 22 April, and of my data, 1 June (table 7). The mean for all these data was 19 May.

The populations of another western woodpecker, the Red-shafted Flicker (*Colaptes auratus cafer*) may be declining (Troetschler 1970, Bock and Smith 1971), perhaps because of competition with Starlings for holes. Data for this species (tables 8, 9) have been in-

TABLE 9. Parameters of habitat utilization by the Acorn Woodpecker, Starling, and Red-shafted Flicker.<sup>a</sup>

A. Height of holes (m)			
	AWP	S	RSF
Mean <sup>b</sup>	17	8	5
Range	3-24	1.5-18	1.5-15
B. Elevation of reproductive range (m)			
	AWP	S	RSF
Mean <sup>b</sup>	676	853	1646
Range	0-1800	0-2400	0 > 2400
C. Breeding habitat (%)			
	AWP	S	RSF
Farms & savannah	16	22	18
Forests	43	16	71
Suburban	35	59	5
Other	5	8	6

<sup>a</sup> As in footnote, table 8.  
<sup>b</sup> All means except AWP-S elevation significantly different ( $P \geq .001$ ) from adjacent items in every direction in the table (anova, Sokal and Rohlf 1969).

cluded, therefore, in an analysis of several factors which may influence the competitive impact of Starlings. I found, as reported by Kessel (1957) and Royall (1966), that egg dates for western Starlings ( $n = 810$ ) show a significant elevational and latitudinal cline (anova,  $P \leq .001$ ), except at very high altitudes and latitudes where often only one brood is reared. The egg dates of the Acorn Woodpecker ( $n = 71$ ) show a similar pattern, again with earlier means from very high elevations reflecting a shorter breeding season. Mean egg dates for Red-shafted Flickers ( $n = 146$ ), however, do not show such clines; the means did not differ significantly at any

TABLE 8. Variation of Acorn Woodpecker, Starling and Red-shafted Flicker egg dates with latitude and elevation.<sup>a, b</sup>

		Mean (range) egg dates <sup>c</sup>			
		Degrees	AWP	S	RSF
By latitude	30-35		5/6(3/1-9/15)	4/10(3/1-5/30)	5/13(4/1-6/30)
	36-40		5/23(3/16-8/30)	4/16(3/16-6/30)	4/26(3/1-6/15)
	41-45		—	3/29(3/1-5/30)	5/9(4/1-6/30)
	46-50		—	no data	5/10(4/1-6/30)
		Meters			
By elevation	0-599		5/23(3/1-9/15)	4/10(3/16-6/15)	4/22(3/1-5/30)
	600-1199		no data	4/17(3/1-5/30)	5/12(4/1-6/15)
	1200-1799		5/8(4/16-6/30)	4/23(3/16-6/15)	5/24(4/16-6/15)
	$\geq 1800$		—	4/19(4/1-5/30)	5/16(4/16-6/30)

<sup>a</sup> Data from North American Nest Record Card Program (1965-73), Royall (1966), Plank (1967), DeHaven and Guarino (1970), works cited in Troetschler (1970), and this study.  
<sup>b</sup> All means except RSF egg dates significantly different ( $P .001$ ) from adjacent items in every direction in the table (ANOVA, Sokal and Rohlf 1969).  
<sup>c</sup> Data grouped in successive 15-day periods.

elevation or latitude. The egg data show that most Acorn Woodpeckers and Red-shafted Flickers begin to breed after Starlings. The egg dates of Starlings and Red-shafted Flickers spanned two to three months, while egg-laying of the Acorn Woodpecker continued for five months.

Similarly, although the ranges of hole heights for the three species overlapped, the means differed significantly (anova,  $P \leq .001$ ); the mean height of *S. vulgaris* nest holes was between those of the two woodpeckers. Starlings use suitable holes at almost any height whereas Acorn Woodpeckers tend to excavate holes near the top of large trees, and Red-shafted Flickers choose the lower trunk and stubs. Most Starlings and Acorn Woodpeckers breed at significantly lower elevations ( $\bar{x} = 840$  and  $670$  m, respectively) than the Red-shafted Flicker ( $\bar{x} = 1620$  m), although Starlings have been reported breeding at all elevations from sea level to over  $2400$  m (table 9B). Finally, although the three species are widely sympatric, they are not equally common in the several habitats where they occur (table 9C). Red-shafted Flickers and Acorn Woodpeckers most commonly are reported from open forest and Starlings from suburban areas. Thus my study-area may be representative of areas where Starling competition is most intense, and woodpeckers in more forested habitats and those at higher elevations may be experiencing less hole competition.

## DISCUSSION

### ACORN WOODPECKER BREEDING STRATEGY

The relatively low fecundity observed for the Acorn Woodpeckers at first presents a paradox. How can a species that breeds only 60% of the time and produces only 0.14 young per adult per year be one of the most "abundant" woodpeckers (Ritter 1938, Bock 1970)? All evidence from the study suggests, however, that the dispersing juveniles were more than sufficient to replace the 10% of the adults dying. A low fecundity which accompanies a long adult life span in a stable environment seems to best characterize the Acorn Woodpecker life strategy.

According to Lack (1954) the life strategy adopted by any species will be that which generates the maximum number of surviving offspring per individual. The evidently successful strategy of the Acorn Woodpecker lends support to models of Cole (1954), Brown (1969), and Roughgarden (1971) who

argued convincingly that selection does not favor earlier maturity or increased clutch size in long-lived species, which do better reproductively by living an extra year. How might such a strategy have arisen in the Acorn Woodpecker?

Group breeding has been observed only in habitats of rather limited diversity. Brown (1969) stated that "shortage of nest space . . . or of good habitat for nest building . . . of heterogeneity in the distribution of food and surplus individuals can lead to selection for polygyny . . ." or for "group territories." Lack (1968) found that unusual breeding patterns, e.g., polygyny and cooperative breeding, were most common among fruit or seed-eaters living in savannah. Verner and Willson (1966) demonstrated that "one-dimensional habitats," i.e., marshes, fields and savannah, are likely to have concentrated areas of food and nest sites. The habitat and major food items of the Acorn Woodpecker fit these conditions. If the available food is clumped and is sufficient to support a larger grouped, rather than non-grouped, population, then selection may favor group behavior, especially if the nest-sites are clumped as well, as they are for any species nesting in dead trees and limbs. To account for group behavior, we need not invoke kin-selection (Hamilton 1964, Brown 1969), although it may be operating, or group selection (Wynne-Edwards 1962, 1965), if group behavior leads to increased survival of a group member who thus leaves more offspring than would his lone counterpart. In the non-family groups observed, however, promiscuity may be a prerequisite for increased fecundity of individuals.

Bock (1970) and MacRoberts (1970) suggested that Acorn Woodpecker groups evolved as an efficient means of defending the food stores which, in turn, function to increase individual survival. Two close relatives of this species, the Red-headed and the Lewis' (*Asyndesmus lewis*) woodpeckers, singly defend stored acorns through the winter. Both exhaust these stores by late spring (Killham 1958b, Bock 1970), and both tend to migrate to new areas for breeding. Usually the acorn stores of the Acorn Woodpecker last until the new crop appears and are used, in addition to flying insects and fruit, as food for both adults and nestlings. It would seem that social groups are more efficient at storing and defending mast than are single woodpeckers. Bock and Bock (1974) suggested that numbers of Acorn Woodpeckers living in the more usual areas, where acorn crop failure is ran-

dom and frequent, are limited by density-independent factors, while those in the few areas with little or no acorn crop failure are limited by density-dependent factors and are extremely abundant. In California areas with low oak-species diversity (as used in this study), Acorn Woodpecker groups may remain for years only in those territories where the acorn crop seldom fails, and social groups may be essential to ensure defense of such premium territories and maximum exploitation of the reliable and concentrated food supply thus obtained. Likewise, it usually would be advantageous for an emigrating bird or group of birds to be accepted in such a "tested" territory rather than pioneering an unknown habitat. By wintering in the few localities where the current acorn crop is unusually large (Kilham 1958b, Bock 1970) the allopatric Red-headed and Lewis' woodpeckers use a superabundant food source fully exploitable only by vagrant species.

Many woodpeckers are reported not to tolerate conspecifics out of the breeding season (Skutch 1943, 1945, Kilham 1958b, 1962, 1969, Lawrence 1966), and it is difficult to imagine cooperative breeding arising in such species. However, the melanerpine woodpeckers exhibit a spectrum of tolerances of mate and offspring from complete intolerance to cooperative breeding. Skutch (1943, 1945) classified the melanerpine woodpeckers according to sociability, and predicted that the colonies of the most social, the Acorn Woodpecker, would consist of family groups which remain together longer than one year. More recently Selander (1966) and Ashmole (1967) proposed conflicting explanations for colonial breeding (the loose colony of Lack 1968) in *Centurus* (or *Melanerpes*) *striatus* of Hispaniola, and Short (1970) reported a similar loose colony, but with possible multiple-adult care, in *Melanerpes cruentatus* of tropical South America. Selander's and Short's reports extend our knowledge of the capacity for conspecific tolerance in the melanerpine woodpeckers, but their observations were too brief to determine if social behavior extends beyond the possible grouped nesting. Certainly the reported habitat and feeding patterns of these two species are different from those of other known social species (Lack 1968).

My data suggest that Skutch's prediction of family groups as the typical Acorn Woodpecker social unit was too limited, although juveniles do not always disperse (M. H. MacRoberts, pers. comm.). The Acorn Woodpecker groups that I saw were formed in sev-

eral ways, and once formed, tended to be long lasting. Further, these groups tended to remain an almost constant size in a particular location. What factors operate to maintain such constancy is not known, but obviously dispersal mechanisms must occur even in social species to maintain gene flow and insure efficient use of the available habitat. Both individual and entire colony dispersal were observed in these groups, and, although intergroup intolerance was extreme, intragroup tolerance ensured cooperation in all life activities and even occasional acceptance of emigrating individuals or retention of fledglings as permanent colony members.

Available data for clutch size (including Peyton 1917, Dawson 1923) suggest that more than one Acorn Woodpecker female may lay in the same nest; up to 17 eggs have been found. Four or five eggs is the usual clutch for one female. Similar scattered reports (Michael 1927, Ritter 1938, Adams 1941) suggest promiscuity, although the evidence is sketchy. Neither M. H. MacRoberts (pers. comm.) nor I observed true copulation, although brief episodes of reverse mounting by all group members in both hetero- and homosexual combinations occurred commonly. However, as I observed no "pair behavior" and no one "dominant male," promiscuity is probable. The models described above predict that in long-lived species little selection for breeding at the youngest possible age will occur. Delayed first breeding has been observed commonly among colonially breeding, but long-lived, sea birds and among group-breeding passerines (Dow 1970). Ligon (1970) reported both delayed breeding and family-group tolerance in the Red-cockaded Woodpecker (*Dendrocopos borealis*). It is possible that in Acorn Woodpeckers age of first breeding may be delayed or may depend on the presence or absence of another bird of the same sex in the group.

Of other birds whose group life strategies have been studied (Brown 1963, 1970, Rowley 1965, Harrison 1969, Dow 1970, Balda and Bateman 1971), the colonial pattern of the Smooth-billed Ani, *Crotophaga ani* (Davis 1940) seems to resemble most closely that of the Acorn Woodpecker. It has similar territory formation, intercolony antagonism, and intracolony tolerance, and probably promiscuous mating with more than one female laying in the same nest. All group members care for the young and defend a year-round territory in a savannah-like habitat. However, they do not defend stored food, and their col-

onies change rapidly in size and composition. Their fecundity, calculated from data in Davis (1940:table 5), is similar to that observed in the Acorn Woodpecker (0.22 fledgling/adult). I further analyzed his data and found that the success of ani groups with more than one female was considerably higher than that of single-female groups (0.3 fledgling/adult and 0.07 fledgling/adult, respectively). In other group-nesting birds it also has been determined that larger groups fledge more young (Rowley 1965, Harrison 1969). In my study of the Acorn Woodpecker no such advantage was found. However, since much larger groups of Acorn Woodpeckers with more than one female have been reported (Leach 1925, Ritter 1938, Skutch 1969), large group size may be found to enhance fecundity. Larger groups also may be found primarily in richer habitats with greater oak-species diversity.

#### STARLING COMPETITIVE SUCCESS

Although Starlings may fly as much as 80 km for food in winter (Hamilton and Gilbert 1969), in the breeding season they are restricted to nearby sources of food (Dunnet 1955, Plank 1967), the larval insect food for nestlings being found at the roots of short grasses in open fields. Thus, although a few Starlings may breed almost anywhere, the bulk of the breeders are found at low elevations in suburbia, on farms, and in savannah. These habitats put them squarely in competition with a considerable segment of the Acorn Woodpecker population, and less so, because of possible elevational differences, with Red-shafted Flickers. However, the length of the Starlings' breeding season is limited and almost synchronous in a given area from year to year. Thus, although Acorn Woodpeckers were unable to keep their holes when competing with Starlings, their much longer and more flexible breeding season enabled them to breed successfully, primarily after the Starlings had finished. Surprisingly, the analysis suggests that egg dates are not later than those in the past. Leach (1925) reported a protracted period of hole digging from February through April. Egg laying did not begin until 1 May. Perhaps this was a common pattern. However, inasmuch as Red-shafted Flicker egg dates are restricted to a two to three month period in much the same interval as the Starling nesting, and flickers seem only barely able to defend their holes (Howell 1943, North American Nest Record Card Program 1965-1963, Plank 1967), habitat separation

may be the primary mechanism maintaining this species in the face of Starling hole competition, although scattered nestings in the major competing habitats may continue. Thus the preliminary evidence of a possible Red-shafted Flicker population decline (Bock and Smith 1971) could reflect a breeding-range restriction directly attributable to Starling competition.

Although my study suggested that fecundity of the local Acorn Woodpecker groups thus far has been unaffected by the Starling, several possible events may change the long-term picture. One unvarying requirement of an Acorn Woodpecker territory is a suitable nest tree. I have documented the proliferation of that which has occurred over the past several years. As Acorn Woodpeckers have not been observed to drill nest holes in other than soft wood, it is entirely possible that the species at present is using the available hole sites at an accelerated rate. Although Ritter (1938) described many holes as common in these colonies, woodpeckers are now less able because of Starling competition to reuse any of these old holes for breeding. Thus, especially in suburban areas where people are most likely to remove dead trees and decaying limbs, lack of nest sites may limit future breeding. Twice already I have observed the Los Altos group leave their territory when no suitable breeding sites were left by Starlings and return in the fall with fledglings for acorn storage and territorial defense through the winter. Such a behavior prevents use of the acorn stores during the breeding season. Similarly, it is possible that the increased hole defense in fall and winter may change the energy budget and prevent adequate acorn storage and defense. The acorn harvest season is relatively short, though its absolute length depends on the diversity of the oak species present and on the microclimates involved. Harvesting is most intense in the fall when large numbers of Starlings are visiting the territories. The Acorn Woodpecker groups must store the mast when it is available, or it will be harvested by competing acorn-storing species (several western jays, squirrels, Lewis' Woodpecker). Potentially, Starlings could even reduce hole access for shelter as at least some Starlings roost in holes throughout the fall and winter in California (Plank 1967). If Starlings should thus disrupt these latter activities, the Acorn Woodpecker adult mortality could increase, ultimately causing a population decline.

## SUMMARY

A six-year study was conducted to determine if competition with Starlings for tree holes is affecting breeding strategy or fecundity of the Acorn Woodpeckers in California. The pattern of Starling visitation to Acorn Woodpecker territories did not vary during six years, but the number of their summer and fall hole visits increased. Starlings were effective competitors for Acorn Woodpecker holes, and the number of individuals breeding increased during the study. The Acorn Woodpecker groups responded to hole loss by excavating more holes, and using various methods that allowed successful breeding. Thus, their fecundity seemed not to have been affected by Starling hole competition, and the local population remained stable. However, their habitat preferences are such that intense Starling hole competition will continue and spread throughout their range. Increased need for hole defense or lack of nest trees may limit Acorn Woodpecker breeding in the future. A number of Red-shafted Flicker-Starling habitat preferences were analyzed. In the future, successfully breeding Red-shafted Flickers may be found primarily in high mountains and forests.

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