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HABITAT AND RESOURCE RELATIONSHIPS IN ACORN WOODPECKERS

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In a recent contribution on geographical ecology, Bock and Bock (1974) discussed Acorn Woodpecker (*Melanerpes formicivorus*) densities in relation to oak species diversity and tree numbers. They concluded that above a limiting threshold of oak diversity the birds did not respond to oak species diversity, and that they showed a density-dependent numerical increase in response to oak abundance. No similar result has emerged from studies of other species-resource relationships.

A related consideration is the relationship between resource dispersion in the habitat, and the type and degree of dispersion of individuals. Horn (1968) argued that clumped nests should accompany exploitation of resources that vary in space and time. Smith (1968) felt that long-term territoriality should accompany use of resources that could be kept from competitors. These propositions follow Brown's (1964) argument that a primary consideration in the evolution of territoriality in birds is the ratio of relative costs to benefits; that is, the "economic defendability" of resources within the territory. The economic formulation has been widely adopted in the socioecological analysis of species-resources relationships (an excellent example is Jarman 1974).

A third consideration particularly related to birds is "niche gestalt" (Svärdson 1949, James 1971, Whitmore 1977). Each species responds to specific, statistically demonstrable habitat characteristics, which often differ from those of closely related species. In this paper I examine the results of Bock and Bock (1974) and consider their conclusions in view of the hypothesis that Acorn Woodpeckers show a niche gestalt and an adaptive response to resource dispersion in the habitat.

Acorn Woodpeckers are interesting for their long-term family units, cooperative raising of young, and food storing behavior. They normally occur in groups with two or more adults, often in large groups with several older offspring. Territories are occupied for long periods, and contain one or more loci of storage holes in which (usually) acorns, walnuts, or other particulate foods are stored. Descriptions of social organization and ethology are given by Ritter (1938) and MacRoberts and MacRoberts (1976).

METHODS

Structure in Acorn Woodpecker habitats was analyzed by a modification of the procedure of James (1971, James and Shugart 1970). Five 0.04-ha circles (ca. 11-m radius) were surveyed for 25 arbitrarily selected woodpecker groups from a series of transects (see below); i.e., 0.2 ha was sampled per group. A "central" circle centered on the main storage site, which is the activity nucleus for a group. The remaining circles were centered 25–30 m from the center of the first circle, along north-south and east-west compass bearings. A circle was often smaller than the crown of a single large tree, and served as a large "point" sample of habitat structure. All five circles were probably on the same territory, since the average distance to the nearest neighboring territory center for 112 California territories was 127 m.

Using a rangefinder, I measured the radius of a circle, the distance between circles, and the height of the tallest foliage. Ground cover data noted only the presence or absence of green vegetation in a 30-cm circle, directly under the points where canopy cover was read. Dead or dry plant material was ubiquitous; I wished to determine whether living ground cover was important. The variables sampled in each habitat circle were: A, number of trees; S, number of tree species; GPERC, fraction of points on ground (of 20 sampled) having green vegetation; CANCO, fraction of points (of 20 sampled) having vegetation directly overhead; CANHT, height of tallest tree in meters; SHRUB, number of stems less than 7.6 cm diameter at breast height (dbh); MULTI, fraction of points (of 20 sampled) with more than one species of vegetation overhead; and TREEA to TREEH, number of stems 7.6–15.2 cm dbh, 15.2–22.9, 22.9–38.1, 38.1–53.3, 53.3–68.8, 68.8–83.8, 83.8–101.6, and greater than 101.6 cm dbh respectively.

I conducted 21 transect surveys of Acorn Woodpecker abundance in California (ssp. *bairdi*) and three in Arizona (ssp. *formicivorus*). In California I made 18 surveys between mid-October 1974 and mid-April 1975, two in late June 1975, and one in late August 1975. Two Arizona surveys were made in late April 1975 and the third in October 1975. I surveyed areas where visible storage sites indicated the presence of Acorn Woodpeckers and where the transect line was approximately flat. Each transect was at least 1 km long; by referring to the map I surveyed a path about 300 m wide. Storage sites (currently used or not) were mapped.

For each woodpecker group encountered I attempted to make a count, considering this accomplished when three successive estimates were the same; this required at least 20 min and in some cases more than an hour. This procedure is relatively accurate for groups of less than about six birds, but underestimates larger groups (judged from three years of observation at one site). I have noted no tendency for Acorn Woodpeckers to be markedly less visible at any season, and all surveys were made during fair weather. Consequently, I believe that at least 90% of the group counts were accurate. The areas in the transects that were visited by the birds and the distributions of trees and topographic features were used to estimate the portion of a transect within each territory. This territory sample does not portray the size of the entire territory for any group, and I did not evaluate the territory area off the transect. The sample was used only as an estimate of the "resources" available to each group. I counted by species (or estimated, if there were many trees) the number of oak trees per sample territory. The storage trees are roughly centered in the territories, and I feel this method of approximating resources is valid for the procedure I used. Woodpecker group numbers per kilometer for 20 locations in Arizona, New Mexico, and Mexico were taken from Marshall (1957: 46).

Oak diversities herein are oak species counts. I designated as *S1* the number of species common to all territories on a transect, and as S2 the number found only on some territories (numerous or not). Similar data for 20 locations in the American southwest were taken from Marshall (1957:10). The oak diversity labeled *S3* is an estimate of the species found near each transect location. If the woodpeckers are responding to an oak diversity other than that on the transect, it should be the total regional oak count. I felt that the smallest area to which I could legitimately ascribe such a count was a circle with a radius of (arbitrarily) 8 km. The botanical sources used in determining S3 are listed in footnotes to Tables 3 and 4. From these sources I compiled a list of oak species that appear to occur less than 8 km from each transect site. For the California sites and for the surveys I conducted in Arizona, I verified the presence of *S3* oaks; some southwestern field surveys by others have verified *S3* counts for some areas, but some of the Sierra Madre *S3* values are estimates only, based on distributions of oaks from nearby surveys.

Tanoak (*Lithocarpus densiflorus*) was considered an oak species.

I analyzed the circle data by paired-mean *t*-tests, contrasting mean values from the central circles ($n = 25$) with means from peripheral circles ($n = 100$), and by principal components analysis. Transect data were subjected to regression analysis.

The hypothesis of random dispersion of Acorn Woodpecker territory centers was tested with a modification of the **R**-value procedure from the nearest-neighbor technique of Clark and Evans (1954), based on ρ, the density of objects in a circle of unit radius. The objects in this case are storage trees. I assumed uniform territory-center densities in the immediate transect areas, and constructed circles with densities equal to those of the transects. If there are N centers in a transect K km long and 0.3 km wide, the territory center density $\rho = N/0.3K = 3.33N/K$; ρ has units of "centers/km^2."

For a randomly dispersed population, the expected value $[E(r)]$ of r_i (the distance from a center to its nearest neighbor) is $0.5\ \rho^{-0.5}$ by definition (Clark and Evans 1954:25). The expected value of r_i also equals $\bar{r}$, the mean distance between centers in a transect. The measure $\mathbf{R} = \bar{r}/E(r)$ is a measure of nonrandomness. $\mathbf{R} = 1$ for a random dispersion; $\mathbf{R} < 1$ with clumping; $\mathbf{R} > 1$ for regular dispersion.

In my sampling, $\bar{r}$ was in meters; it is divided by 1,000 to conform with ρ. The **R**-value (after several algebraic manipulations) is finally

$$\mathbf{R} = 3.64 \times 10^{-3}\ \bar{r}\ (N/K)^{0.5}.$$

Clark and Evans gave a significance test for **R** based on large samples. While not exact for small samples, it suggests the significance level attained. The measure (C), modified for my procedure, is

$$C = (3.83 \times 10^{-3}\ \bar{r}\ \rho^{0.5} - 1.92)\ N^{0.5}$$

which is distributed approximately as the standard normal curve.

RESULTS

HABITAT STRUCTURE

The hypothesis that Acorn Woodpeckers have uniform habitat says that: (1) the physical habitat is uniform, and (2) use by the birds is nonselective. If the physical habitat is uniform throughout, the important structural variables should be the same for different subsets of habitat data. The circle samples were subjected to principal components extraction: (1) with all circles combined, (2) with central circles deleted, and (3) with only central circles. The three component sets were very similar. I interpreted this result to mean that there are no intrinsic differences among subsets of structural data.

Significant mean differences were found for several variables between the central circles and the rest of the territories (Table 1). The central areas have more tree species (but not more oak species), a higher percent canopy cover, higher canopy, and more trees of moderate to (especially) large size. The fundamental difference between central and peripheral circles is that each central circle includes the storage tree of a woodpecker group, which generally also contains the roosting and nesting cavities for the group. This means that the

TABLE 1. Mean values of each variable from central circles and surrounding area for all territories.

Variables	Central area	Surrounding area
A	7.84	4.76
S*	3.08	1.54
GPERC	33.80	37.80
CANCO*	74.00	36.50
CANHT*	24.42	11.50
MULTI*	16.00	3.15
SHRUB	9.72	5.11
TREEA	4.92	2.59
TREEB	2.44	1.48
TREEC*	2.12	1.35
TREED	0.80	0.64
TREEE	0.32	0.29
TREEF*	0.48	0.14
TREEG[a]	0.28	0.03
TREEH*	0.40	0.03

* $P < 0.05$.

[a] Not significantly different because of large standard errors.

TABLE 2. California data used in testing dispersion of territory centers.[a]

Location[b]	$\bar{r}$ (meters)	N	K	ρ	**R**	C	P
A1	253.63	5	1.56	10.67	1.66	2.81	0.004
ED1	178.32	9	1.80	16.65	1.46	2.61	0.009
ED2	201.42	6	1.20	16.65	1.64	3.02	0.002
ED3	134.68	8	1.40	19.03	1.18	0.95	0.342
LA1	190.24	5	2.10	7.93	1.07	0.31	0.756
M1	227.09	7	1.40	16.65	1.85	4.32	0.001
N1	200.96	7	1.85	12.60	1.43	2.16	0.031
N2	264.46	7	2.10	11.10	1.76	3.86	0.001
N3	274.06	7	1.75	13.32	2.00	5.06	0.001
N4	162.93	5	1.50	11.10	1.09	0.37	0.734
N6	387.50	4	1.66	8.02	2.20	4.57	0.002
S1	294.86	4	1.35	9.87	1.86	3.26	0.012
Y1	183.78	7	1.49	15.64	1.45	2.30	0.022
Y2	209.66	8	1.51	17.64	1.76	4.12	0.001
Y3	226.93	6	2.00	9.99	1.43	2.04	0.042
Y4	267.83	4	2.10	6.34	1.35	1.33	0.184

[a] $\bar{r}$ is the mean distance to nearest neighbor in each transect; N the number of woodpecker groups; K the transect length in kilometers; ρ the density of territory centers per square kilometer. **R** indicates randomness in the dispersion (see text). C is a parameter reflecting the probability (P) of encountering such large **R**-values by chance (see Methods).

[b] Transects were conducted at the following locations: A1, Irish Hill Road, Amador County; C1, Bear Creek, Colusa Co.; ED1, So. Shingle Road, El Dorado Co.; ED2, Greenstone Road, El Dorado Co.; ED3, Latrobe Creek, El Dorado Co.; H1, Chezem Road, Humboldt Co.; K1, Fort Tejon, Kern Co.; LA1, Baldy Village, Los Angeles Co.; M1, Tan Oak Park, Mendocino Co.; N1, Monticello Road, Napa Co.; N2, Wragg Canyon Road, Napa Co.; N3, Sage Canyon, Napa Co.; N4, Aetna Springs Road, Napa Co.; N5, Ink Grade, Napa Co.; N6, White Cottage Road, Napa Co.; S1, Ancil Hoffman Park, Sacramento Co.; SD1, Cuyamaca Rancho State Park, San Diego Co.; Y1, Road 29 (e. section), Yolo Co.; Y2, Road 29 (w. section), Yolo Co.; Y3, Capay Valley, Yolo Co.; Y4, Taylor Canyon, Yolo Co.

woodpeckers are associated with a subset of their habitat that is significantly different from the overall habitat. The structural similarities are important; the habitat matrix has equally large trees, but their frequency is far below that of the central circles.

DISPERSION

I tested whether the dispersion of group centers in space was random with the data and parameters in Table 2, representing the 16 California transects with four or more groups. All **R**-values are greater than 1.0, indicating regular dispersion. The approximate probabilities of encountering such **R**-values by chance are shown in the last column. I conclude that within suitable habitats Acorn Woodpecker territory centers are regularly spaced.

If larger woodpecker groups command larger territories, then the distance to nearest neighbor should correlate with group size. The correlation coefficient r equals 0.008, not significantly different from zero. I infer that territory area is not strongly related to group size. MacRoberts and MacRoberts (1976) found a positive rank correlation between group size and total territory area, but the relationship did not always hold, especially for small groups.

TABLE 3. Oak diversities and bird abundances for California transects.[a]

Location[b]	Oak diversity[c] S1	S2	S3	N_t	G	D
A1	2	2	4	18	5	1.56
C1	2	3	4	6	3	1.69
ED1	2	4	5	24	9	1.80
ED2	4	4	8	18	6	1.20
ED3	2	3	5	23	8	1.40
H1	3	4	4	5	2	1.43
K1	2	2	8	13	3	1.37
LA1	1	3	5	18	5	2.10
M1	3	4	5	28	7	1.40
N1	4	7	8	20	7	1.85
N2	5	6	7	16	7	2.10
N3	3	4	6	21	7	1.75
N4	2	3	6	14	5	1.50
N5	4	5	10	9	2	1.37
N6	2	5	10	20	4	1.66
S1	2	2	3	20	4	1.35
SD1	3	4	6	15	3	1.59
Y1	3	3	4	22	7	1.49
Y2	3	3	4	29	8	1.51
Y3	2	3	3	17	6	2.02
Y4	2	3	3	14	4	2.10

[a] N_t is the total bird count; G the number of groups; D the transect length in kilometers.

[b] Location codes in footnote of Table 2.

[c] S3 oak diversities were calculated by enumeration from oak distributions in Griffin and Critchfield (1972), McDonald (1969), McMinn (1951), Munz and Keck (1959), and Twisselmann (1967); see Methods.

ECOLOGICAL FACTORS

Oak diversities and woodpecker abundances for the California and some Arizona sites are presented in Tables 3 and 4. Marshall's (1957) tabular data are presented only for the three mountain ranges I also surveyed; the remaining values are available in Marshall's Tables 1 and 3, except S3 diversity values, which are listed in a footnote to my Table 4.

I evaluated the hypothesis that woodpecker densities were a function of oak species diversity. There were no significant regressions of groups/km or birds/km for the California data; a plot of groups/km versus S3 oak diversity is shown in Figure 1. Several linear transformations of the data were no more effective, and the scatter in the data made it appear unlikely that nonlinear functions of oak diversity would provide a better regression.

In contrast, the regression of groups/km

TABLE 4. Oak diversities and woodpecker abundances for three Arizona mountain ranges.[a]

	Oak diversity[b]					
	S1	*S2*	*S3*	*G*	N_t	*D*[c]
Santa Catalina[d]	3	3	7	1.86	n.a.[c]	n.a.
Santa Rita [d]	3	3	6	1.24	n.a.	n.a.
Chiricahua[d]	3	3	11	1.86	n.a.	n.a.
Santa Catalina[e]	4	4	7	4.93	23	1.42
Santa Rita[e]	3	4	6	2.67	13	1.50
Chiricahua[e]	3	5	11	1.58	24	3.17

[a] *G* is woodpecker groups per transect kilometer (different from Table 3); N_t bird total per transect; *D* transect length in kilometers.

[b] See Methods for derivation of oak diversities. *S1* and *S2* values for 17 other southwestern mountain ranges in Marshall (1957:10). *S3* values for those sites are: Pinaleno, 7; Huachuca, 9; Cananea, 7; Ajos, 7; Peloncillo, 5; San Luis, 5; Pulpito, 6; Pinitos, 5; Azul, 6; Aconchi, 9; Oposura, 7; El Tigre, 10; Huachinera, 13; Nacori, 13; Sierra Madre: high, 14; west, 13; east, 12. Sources for *S3* diversities are Brand (1936), Kearney and Peebles (1951), Leopold (1950), Little (1950, 1953), Muller (1951), Shreve (1915), Wallmo (1955), and White (1948).

[c] n.a. = not available from Marshall's data.

[d] From Marshall (1957), except *S3*.

[e] From 1975 survey.

against *S3* diversity for the Arizona-New Mexico-Mexico data is significant (Fig. 2). There is also a significant regression of groups/km against *S2* diversities ($G = 0.82\ S2 - 0.53$; $F_{1,21} = 5.71$; $P < 0.05$). The southwestern data therefore support the hypothesis that bird densities respond to oak species diversity.

Bock and Bock (1974) proposed a linear relationship between bird numbers and resource abundance, measured as a percentage of sampled habitat containing oaks. A measure of an actual resource (acorns) might be approximated by a count of the items from which the resource comes (i.e., the oaks). For the California transects, the equation regressing the number of woodpeckers in a group (*N*) on the number of oak trees in their territory sample (*T*) is $N = 0.014\ T + 2.8$. The regression coefficient is not statistically different from zero. Since the distance between centers is not a function of group size, the tendency for larger groups to have more trees suggests that group size might respond to tree density, a result that would support the Bock and Bock (1974) hypothesis. The form of this relationship in the southwestern sites is unknown.

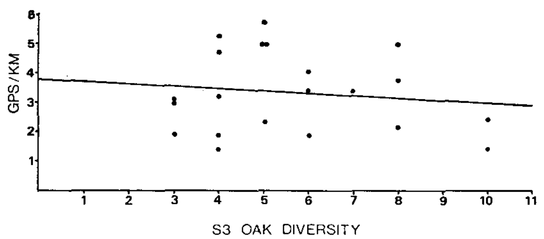

FIGURE 1. California values of *S3* oak diversity and woodpecker groups per transect kilometer. The least-squares fitted regression line is $G = 3.75 - 0.08$ *S3*; statistically there is no relationship between oak diversity and woodpecker density.

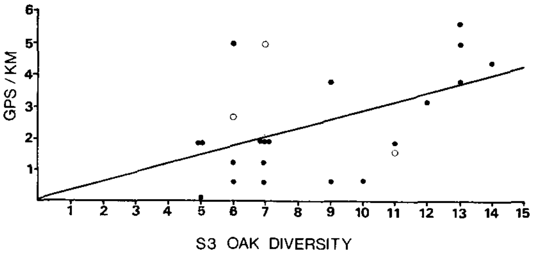

FIGURE 2. Southwestern values of *S3* oak diversity and woodpecker groups per transect kilometer (mostly derived from Marshall 1957). The fitted regression line is $G = 0.28\ S3 + 0.04$; $F_{1,21} = 6.91$, $P < 0.05$. The three open circles represent the mountain ranges I sampled; Marshall's values for those ranges are listed in Table 4 and also plotted here.

DISCUSSION

HABITAT AND THE NICHE GESTALT

Acorn Woodpecker densities are conceptually related to habitat structure in two ways. First is the close association of a woodpecker group with a habitat portion quantitatively different from the habitat not so used. There is a related qualitative difference: territory centers are "traditional" storage sites. The large trees, often but not always pines, have dead wood and/or thick bark that can be converted to storage sites. Cracks are often used for storage, but most often holes are drilled, a process that may require months since holes are made in many small steps. Holes are energetically expensive, and storage loci are infrequently moved. Acorn Woodpeckers may ignore potential hole substrate in other parts of their territory in favor of expansion of an extant storage locus. Acorns are harvested from oaks everywhere on a territory, and are usually brought to the central tree for consumption or storage. Flyways into the anvils and storage areas are open, and the storage loci are visible at a distance. Other large trees on woodpecker territories may equal the central trees in stature, but lack the modifications. Published descriptions from the species' entire range indicate that mixed pines and oaks comprise Acorn Woodpecker habitat as far south as pines occur, and habitat south of that is open woodland similar in structure to pine-oak (summary provided on request). The clear quantitative and qualitative association of woodpecker groups with large, emergent trees in habitats of particular structure is consistent with the concept of niche gestalts.

The second element in the woodpeckers' habitat response is the regular spacing of storage/activity centers, and the associated territoriality. Regular spacing limits the number of sites at which storage loci could be established; suitable trees not sufficiently near a territory center may be ignored. Territoriality limits the indefinite increase in group numbers in an area, regardless of oak species diversity. However, since resources may be differentially packed into territories, bird numbers might respond to tree density, productivity, or related phenomena. Larger groups also might usurp space from smaller groups (MacRoberts and MacRoberts 1976), but because of the group-centroid spacing, smaller groups are at a relative advantage in holding their territories. Acorn Woodpecker resource exploitation and social behavior are evolutionarily linked to the habitat structure that is the niche gestalt (see below).

THRESHOLDS

A major factor in the Bock diversity-density model is a threshold of oak species numbers at which woodpecker numbers increase rapidly from near zero to a nearly constant level, at about four species in California and six or seven species in the southwest. My results generally support the hypothesis.

In the Bock model, more oak species render less likely a complete acorn failure on a site. "Random but frequent acorn crop failures" (Bock and Bock 1974:696) are postulated at low oak diversities, but above a species threshold the probability of total failure becomes low enough that woodpeckers are essentially certain to find acorns. Little evidence is available to evaluate these assumptions. The effect of area-wide, adverse conditions on acorn productivity in different oak species is unmeasured. I suspect that adverse climatic conditions, which would increase the probability of acorn failure, should increase with latitude within the range of each oak species. Also, oak growth forms generally become more shrublike near the higher altitudinal and latitudinal limits of a species (Muller 1951). Thus the probability of insufficient food and the disappearance of properly conformed habitat should both increase with latitude in the United States. Low densities of woodpeckers in areas of low oak diversity could be due to either low productivity or a poor niche gestalt, or both. The California habitat patches I sampled appear to be above any oak diversity threshold, and show properly conformed habitat.

Pine-oak woodland is restricted to higher elevations in the American southwest, so there may be qualitative differences between habitats there and in California. In southern Arizona the abundances of oak species are approximated by a set of overlapping curves along a steep gradient up a mountainside (Whittaker and Niering 1965). My observations and Marshall's data indicate that only a part of the altitudinal range and the included oak species are within habitats normally occupied by Acorn Woodpeckers. In California there are generally larger expanses of oak-containing habitat and less-steep altitudinal gradients, and areas of geographical overlap are more extensive. Nonetheless, it is unlikely that individual woodpeckers "see" more oak species than in Arizona; *S1* and *S2* values in Table 3 are essentially the same as in Marshall's results (1957:10). Oak species appear more numerous in the Sierra Madre of northern Mexico, but I do not know the patterns of oak distribution and acorn production found there. Those habitats, where S3 diversity is above 11 oak species, provide the basis for the positive regression of Fig. 2; they are also clearly above the "threshold" of oak diversity needed to maintain high Acorn Woodpecker densities.

TERRITORIES AND RESOURCES

Acorns appear to be the most important resource for Acorn Woodpeckers. Acorn production by individual oaks is irregular in both space and time (Griffin 1971, 1976). Horn (1968) suggested that the optimum point for efficient ranging should be a central site that minimizes the second moment of foraging flights. Smith's (1968) analysis of squirrel foraging indicated that with particulate resources such as acorns, the point should be at the center of a circular range. From this model, the most efficient use of variable acorn crops by Acorn Woodpeckers should occur with a circular range having a storage site near the center. However, if the pattern of acorn production is considered over a large habitat region, the spatial distribution of acorns should be more nearly uniform. Woodpecker social units might best harvest this resource by being regularly dispersed.

Considered on these scales, it appears that Acorn Woodpecker territories are shaped in accordance with an hypothesis of highest "economic" efficiency in acorn harvesting, at least in the sites I studied. Other resources may have similar distributions. Tree-related resources such as sap and tree-borne insects may be considered to be more or less uniformly distributed, and the regular dispersion of territory centroids should maximize harvest efficiency in their consumption. Further development of this analysis must await actual measurements of resource distribution and production on a microhabitat basis.

I could detect no qualitative differences in behavior or ecology between birds in California and Arizona. Skutch (1969) described territoriality in a group of five birds in Costa Rica, and harvesting and storing behavior in Guatemala. He showed a photograph from Honduras of acorns stored in a pine trunk. Eisenmann (1946) observed acorn storing in Panama, and Peck (1921) described it in British Honduras (Belize). A. H. Miller (cited in MacRoberts and MacRoberts 1976: 27) noted storage holes in tall, dead trees in Colombia. There appears to be little difference in these aspects of Acorn Woodpecker biology over a very large area. Similarities among habitats occupied by these different populations were noted above. From these observations I deduce similar sets of local conditions throughout the species' range.

The distribution of pine-oak woodland on mountain slopes in the southwest has allowed the habitat to shift up- or downslope as climatic conditions have changed, in addition to long-term evolutionary changes in the plant community (Axelrod 1958). Provided that the change is gradual, an area of habitat could retain some woodpeckers as it changed from suitable to marginal habitat. As the change continued I would expect the ecological factors under which Acorn Woodpeckers evolved to change as well, and possibly to produce notable differences in woodpecker ecology and behavior. A recent study (C. E. Bock, pers. comm.) of Acorn Woodpeckers in southern Arizona supports this expectation: habitat structure is very different from pine-oak woodland, few birds occur in long-term groups, and some woodpeckers seem to migrate seasonally.

The evolutionary basis for this change is presently unclear. However, individual Red-headed (*Melanerpes erythrocephalus*) and Lewis' (*M. lewis*) woodpeckers normally winter and store opportunistically in places where mast is abundant (Bock and Lepthien 1975; also see Roberts, in press). I suggest that the averaged productivity of all food sources is the winter density-determining criterion for all three species. If individuals were able to interchange resources from different food sources, total densities should be correlated with annual production of all resources. For example, some finches select seeds on the basis of size (Pulliam and Enders 1971, Willson and Harmeson 1973, Pulliam 1975), and population sizes in several Arizona sparrow species were functions of overall sizes and availabilities of seeds (Pulliam 1975). Similarly, Acorn Woodpeckers in a site in New Mexico store and subsist on piñon (*Pinus edulis*) seeds as well as acorns (Stacey and Jansma 1977). Foods of both woodpeckers and finches are particulate and are produced in regular (i.e., predictable) seasonal pulses. Other groups of temperate-zone wintering birds (e.g., jays) and mammals (e.g., some rodents) probably respond similarly.

Foraging behavior, nest-site selection, and anti-predator behavior are related to the habitats in which a species evolves. Replacements among species depend upon evolutionary associations between species and habitats (Salt 1953, Johnson 1966). Theories of socio-ecology (e.g., Jarman 1974) indicate that selection operates on social behavior concurrently with resource distribution and other factors. The territorially-based regular dispersion of Acorn Woodpecker storage sites enhances each individual's potential for exploiting the environment. Long-term territoriality also limits the potential for establishing new territories, a factor that Brown (1974) implicated in the evolution of sociality in Mexican Jays (*Aphelocoma ultramarina*) and I elsewhere (1976) invoked for *M. formicivorus*. Geographical variation in ecological factors underlying social behavior suggests that such behavior could be highly variable in expression. However, highly adaptive social organizations apparently subsume a great deal of variation in underlying ecological factors, and the expected variation is not often observed. Comparative and synthetic research in avian socioecology is clearly needed.

SUMMARY

Acorn Woodpecker densities on 21 California transects were not significantly correlated with oak species diversity, but woodpecker densities taken from the literature for 20 sites in the American southwest and Mexico were positively correlated with two measures of oak diversity. All transects were in pine-oak woodland or similar sites, indicated in the literature as good habitat for Acorn Woodpeckers. Physiognomic habitat samples from 25 territories indicated that woodpecker groups were associated with large, high-canopied trees (most often pines in the territories

studied), which the birds modified into storage centers. In 12 of the 16 transects tested, these centers were regularly dispersed. These results are consistent with an interpretation of saturation of these favorable habitats.

An analysis of these results and the foraging and social behavior of Acorn Woodpeckers suggests that the birds respond to a specific niche gestalt. A central activity locus theoretically optimizes foraging-flight efficiency when fluctuating resources such as acorns are harvested from each territory. This is consistent with the view that Acorn Woodpecker territories are "economically" defendable.

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LITERATURE CITED

Axelrod, D. I. 1958. Evolution of the Madro-tertiary geoflora. Bot. Rev. 24:433–509.

Bock, C. E., and J. H. Bock. 1974. Geographical ecology of the Acorn Woodpecker: diversity versus abundance of resources. Am. Nat. 108: 694–698.

Bock, C. E., and L. W. Lepthien. 1975. A Christmas-count analysis of woodpecker abundance in the United States. Wilson Bull. 87:355–366.

Brand, D. D. 1936. Notes to accompany a vegetation map of northwest Mexico. Univ. New Mexico Bull. Biol. Ser. 280:1–27.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160–169.

Brown, J. L. 1974. Alternate routes to sociality in jays—with a theory for the evolution of altruism and communal breeding. Am. Zool. 14:63–80.

Clark, P. J., and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445–453.

Eisenmann, E. 1946. Acorn storing by *Balanosphyra formicivora* in Panama. Auk 63:250.

Griffin, J. R. 1971. Oak regeneration in the upper Carmel Valley, California. Ecology 52: 862–868.

Griffin, J. R. 1976. Regeneration in *Quercus lobata* savannas, Santa Lucia Mountains, California. Am. Midl. Nat. 95:422–435.

Griffin, J. R., and W. B. Critchfield. 1972. The distribution of forest trees in California. U.S. Dep. Agric. For. Serv. Res. Pap. PSW-82. Pacific SW. Forest and Range Exp. Stn., Berkeley.

Horn, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird (*Euphagus cyanocephalus*). Ecology 49:682–694.

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83:215–236.

James, F. C., and H. H. Shugart. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. Behaviour 58:215–267.

Johnson, N. K. 1966. Bill size and the question of competition in allopatric and sympatric populations of Dusky and Gray flycatchers. Syst. Zool. 15:70–87.

Kearney, T. H., and R. H. Peebles. 1951. The flora of Arizona. Univ. California Press, Berkeley.

Leopold, A. S. 1950. Vegetation zones of Mexico. Ecology 31:507–518.

Little, E. L., Jr. 1950. Southwestern trees—a guide to the native species of New Mexico and Arizona. U.S. Dep. Agric. Handb. No. 9. Government Printing Office, Washington, D.C.

Little, E. L., Jr. 1953. Check list of the native and naturalized trees of the United States (including Alaska). U.S. Dep. Agric. Handb. No. 41. Government Printing Office, Washington, D.C.

MacRoberts, M. H., and B. R. MacRoberts. 1976. Social organization and behavior of the Acorn Woodpecker in central coastal California. Ornithol. Monogr. 21:1–115.

Marshall, J. T., Jr. 1957. Birds of pine-oak woodland in southern Arizona and adjacent Mexico. Pac. Coast Avif. 32:1–125.

McDonald, P. M. 1969. Sylvical characteristics of California black oak (*Quercus kelloggii* Newb.). U.S. Dep. Agric. For. Serv. Res. Pap. PSW-53. Pacific SW. Forest and Range Exp. Stn., Berkeley.

McMinn, H. E. 1951. An illustrated manual of California shrubs. Univ. California Press, Berkeley.

Muller, C. H. 1951. The oaks of Texas. Contrib. Texas Res. Found. 1:21–309.

Munz, P. A., and D. D. Keck. 1959. A California flora. Univ. California Press, Berkeley.

Peck, M. E. 1921. On the acorn-storing habits of certain woodpeckers. Condor 23:131.

Pulliam, H. R. 1975. Coexistence in sparrows: a test of community theory. Science 189:474–476.

Pulliam, H. R., and F. Enders. 1971. The feeding ecology of five sympatric finch species. Ecology 52:557–566.

Ritter, W. E. 1938. The California Woodpecker and I. Univ. California Press, Berkeley.

Roberts, R. C. 1976. Ecological relationships in the Acorn Woodpecker (*Melanerpes formicivorus*). Ph.D. diss., Univ. California, Davis.

Roberts, R. C. The evolution of avian food storing behavior. Am. Nat., in press.

Salt, G. W. 1953. An ecological analysis of three California avifaunas. Condor 55:258–273.

Shreve, F. 1915. The vegetation of a desert mountain range as conditioned by climatic factors. Carnegie Inst. Washington Publ. No. 217.

Skutch, A. F. 1969. Life histories of Central American birds, part III. Pac. Coast Avif. 35: 1–580.

Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels, *Tamiasciurus*. Ecol. Monogr. 38:31–63.

Stacey, P. B., and R. Jansma. 1977. Storage of piñon nuts by the Acorn Woodpecker in New Mexico. Wilson Bull. 89:150–151.

Svärdson, G. 1949. Competition and habitat selection in birds. Oikos 1:157–174.

Twisselmann, E. C. 1967. A flora of Kern County, California. Univ. San Francisco Press, San Francisco.

Wallmo, O. C. 1955. Vegetation of the Huachuca Mountains, Arizona. Am. Midl. Nat. 54:466–480.

White, S. S. 1948. The vegetation and flora of the region of the Rio de Bavispe in northeastern Sonora, Mexico. Lloydia 11:229–302.

Whitmore, R. C. 1977. Habitat partitioning in a community of passerine birds. Wilson Bull. 89: 253–265.

Whittaker, R. H., and W. A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. Ecology 46:429–452.

Willson, M. F., and J. C. Harmeson. 1973. Seed preference and digestive efficiency of Cardinals and Song Sparrows. Condor 75:225–234.

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RECENT PUBLICATIONS

Appendicular Myology and Relationships of the New World Nine-primaried Oscines (Aves: Passeriformes).—Robert J. Raikow. 1978. Bull. Carnegie Mus. Nat. Hist. No. 7, Pittsburgh. 43 p. Paper cover. $3.50. Available: Carnegie Mus. Nat. Hist., 4400 Forbes Ave., Pittsburgh, PA 15213. This paper presents the results of an attempt to analyze the evolutionary relationships in a large assemblage of songbirds, based on the gross morphology of the forelimb and hindlimb muscles. Raikow suggests that "the Parulidae are the most primitive family of the group, the Thraupidae somewhat more advanced, and the Fringillidae and their descendents the most highly derived." The affinities of the vireos are still obscure. This is a clearly-written, though technical, report which will be of value to systematists.

Fauna Sinica, Series Vertebrata, Aves, Vol. 4: Galliformes.—Cheng Tso-hsin et al. 1978. Science Press, Academia Sinica, Peking, China. 203 p. The *Fauna Sinica* is a very ambitious project now underway (see the Special Report, p. 104–109) to survey the entire fauna of the People's Republic of China. This is a volume in that series, a general summary of present knowledge about the country's 56 species of gallinaceous birds. It was essentially finished in 1975 but publication was delayed by political problems. A general introduction presents the entire order and lists the species in the PRC. The species accounts include distribution, field marks, detailed description, subspecies, and habits. Many keys to species and subspecies are given, and taxonomic relationships are discussed frequently. The list of references shows that Cheng and his five co-authors have been familiar with western ornithological literature, even in recent years. Illustrated with range maps, phylogenetic diagrams, and color plates. The book will be useful to researchers who are interested in the systematics and habits of the Galliformes—if they can read Chinese.

Behavioural Ecology: An Evolutionary Approach.—Edited by J. R. Krebs and N. B. Davies. 1978. Sinauer Associates, Inc., Sunderland, MA. 494 p. Hard cover $34.00, paper cover $17.50. The interactions among ethology, ecology, and the theory of natural selection during the past 25 years have created one of the most seminal and exciting areas in zoology. This textbook discusses some of theoretical ideas, observations, and data that have emerged here. Topics covered include predator-prey relationships, social organization, sex and choice of mates, communication, territoriality, habitat selection, decision-making, and life history patterns. Overlaps, duplications, and differences in style are inevitable in a book whose chapters are written by many different authors, but in the present case they are not bothersome. Mercifully, graphs are used instead of complex mathematical theory wherever possible. Although the book was planned for higher level undergraduates, it is certainly not too elementary for graduate students. Its many new ideas and reviews will interest researchers and teachers, especially those who feel a need to be brought up to date.