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11. We thank Walter W. Stewart for the gift of lucifer yellow, Georgia Harper and Ellis N. Story for technical assistance, and Juan Fernandez and Eduardo Macagno for helpful suggestions and discussions. Supported by NIH postdoctoral fellowship NS05445, by NIH research grant NS 12818, and by NSF grant BN 574-2437 A02.

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Social Plasticity in the Acorn Woodpecker

Abstract. *Acorn woodpeckers (*Melanerpes formicivorus*) in southeastern Arizona exhibited two different types of social organization: one of highly cooperative and resident groups and another of birds that migrated and formed only temporary male-female pairs during reproduction. The occurrence of both patterns in the same population indicates a high degree of social flexibility in this species.*

The acorn woodpecker (*Melanerpes formicivorus*) has one of the most unusual social organizations of any North American bird. Individuals live in permanent groups containing as many as 12 adult members (*1*). The groups occupy and defend year-round territories, and they breed communally; most or all of the adult members help to feed the young of a single nest. Another distinctive feature of this species' behavior is its extensive dependence upon stored mast. Acorns and other nuts are collectively harvested by the groups in the fall and stored in individual holes that have been made by the woodpeckers. The storage holes usually are concentrated in one or two trees on the group's territory, and the stored mast forms an important food resource during the winter. This type of group social organization and mast storage behavior has been reported for all locations in which the acorn woodpecker has been observed, including a number of areas in California (*1, 2*), in New Mexico and Arizona (*3*), as well as in Mexico (*4*) and parts of Central America (*5*). We now describe a population of acorn woodpeckers in southeastern Arizona in which most of the woodpeckers exhibited an entirely different form of social organization and ecology than that described earlier. Some individuals in this area, however, behaved like the acorn woodpeckers observed previously. The coexistence of two different types of social organization within the same population indicates that the acorn woodpecker can be extremely flexible in its social behavior.

We observed the acorn woodpeckers at the Research Ranch, Elgin, Arizona, 85 km southeast of Tucson. The main study area was in an oak savanna and oak woodland (*6*). Additional observations were made in a number of locations in the nearby Huachuca Mountains. The study was conducted in January 1975, May through August 1975, January and March 1976, and May 1976 through March 1978. During this period 63 adults and juveniles were marked with individually color-coded leg bands and wing tags.

Unlike the acorn woodpeckers studied elsewhere, the majority of birds at the Research Ranch did not construct acorn storage holes and their territories did not contain storage trees. The woodpeckers did store acorns, but the nuts were placed under loose bark and in natural crevices of oak trees and power poles throughout their territories. In most years, these stores were exhausted soon after the oaks ceased acorn production. The woodpeckers then abandoned their summer territories and briefly wandered over the study area before they disappeared. At the same time, a number of transient and solitary individuals moved through the area from other locations. By early winter, almost all of the acorn woodpeckers had left the study site and surrounding areas. The abandoned territories remained unoccupied during the winter. In the spring, birds returned and established new breeding territories. During the winter of 1976–1977, for example, only one of 12 summer territories was occupied between December and March. Ten of these territories were reoccupied by woodpeckers in the following spring.

Some of the acorn woodpeckers that established breeding territories on the study site during the spring had been present in previous summers (Table 1); most of the adults occupied the same territories that they had held the year before. In general, territories were established in the same locations each year, although often by new birds.

Although we do not know where the acorn woodpeckers that leave the Research Ranch spend the winter (*7*), the regular abandonment of summer breeding territories over large areas, absence during the winter, and reoccupation during the spring suggest that these individuals do indeed migrate. The pattern of behavior observed during this study is not a recent occurrence; similar seasonal movements of acorn woodpeckers were reported in the adjacent Huachuca Mountains in 1904 (*8*).

The migratory acorn woodpeckers exhibited a radically different form of social organization than that previously described for this species. Many of the differences seem to be the result of a lack of stable, long-term bonds between individ-

Table 1. The behavior of acorn woodpeckers in the winter and summer that followed the breeding season in which they were color-banded. The table includes individuals banded during 1975 and 1976; it does not include six birds captured in the summer of 1977.

Behavior	Adults	Juveniles	Transients*
Migrated and returned to same territory the following year	7	1	
Migrated and returned to different territory the following year	2	0	
Winter resident in resident group	2	0	
Solitary winter resident	0	0	1
Did not return in first year but returned in second year	1	0	0
Transients that migrated and then returned to breed in area			2
Disappeared and were not seen again	18	13	10
Total	30	14	13

*Transients are individuals that did not breed in the study site but moved into the area and were captured prior to the fall migration.

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uals. The majority of birds did not breed in communal groups but in simple male-female pairs. The largest group observed at the Research Ranch during this study contained only three adult members (Table 2). The pairs appeared to be only temporary reproductive associations. The birds usually dispersed individually in the fall, and one member of the pair often left before the other member. There was little fidelity between mates, as no marked individual was observed to breed twice with the same partner. In only one case did both members of a banded pair return; the male reoccupied his old territory but mated with a new female, while the female moved to a different territory and joined a new male. We found no evidence of extended bonds between parents and their offspring. Juveniles often dispersed before their parents in the fall, and only one juvenile returned to the same area in which he had been born (Table 1). The woodpeckers were also able to form temporary associations with other individuals, both prior to pair formation in the spring and before migration in the fall (*9*). In many ways, the social organization of these birds is similar to that of nonsocial migratory wookpeckers that are closely related to the acorn woodpecker (*10*).

Long-term bonds between individual birds are one of the most characteristic features of the social organization of the acorn woodpecker in other regions. Many birds in these populations remain within the same group for extended periods, and some individuals may spend their entire lives with a single group on the same territory. Juveniles regularly remain with their parental groups during their first winter, and they can become permanent members of those groups (*1*, *3*). Individuals may change groups, but once they do so, they treat all other woodpeckers, including members of their old group, as outsiders (*3*).

Although most of the acorn woodpeckers we observed at the Research Ranch followed the nonsocial migratory strategy described above, small groups of two to four adults were permanent residents throughout the course of the study. The birds in these groups behaved in almost every way like the acorn woodpeckers found elsewhere. Most of the resident groups occurred in the pine-oak belt of the adjacent mountain ranges (*11*); a few were also found in oak woodlands and oak savannas. In 1976 and 1977, we censused the main study area and an additional 12 km of canyon bottoms and oak woodlands in the foothills of the Huachuca Mountains. This area

Table 2. Number of adults in breeding groups of acorn woodpeckers at the Research Ranch, southeastern Arizona.

Year	Pairs	Groups of three	Average
1975	7	2	2.22
1976	10	2	2.17
1977	10	1	2.09

contained numerous pairs of acorn woodpeckers during the summer that subsequently migrated in the fall. However, we found five groups that remained on their territories throughout the winters of both years. In contrast to the migratory birds, all of these resident groups had large storage trees or other mast storage facilities. These facilities allowed the groups to store large numbers of acorns in the fall and to efficiently protect the stores from competitors (*12*). The stored acorns provided food for the groups during the winter. Significantly, three of the five groups also were able to obtain food from dog bowls and bird feeders at local ranches. Some of the juveniles fledged by these groups remained on their natal territories during the winter; none of these birds were banded but most apparently dispersed in the spring. One of the groups (on the main study area) contained two adult males and one adult female during the three breeding seasons of this study. The members of this group bred communally; all of the adults helped to feed the nestlings.

The two forms of storage behavior and social organization occurred together in the same population and were observed in woodpeckers that occupied adjacent territories. In addition, some birds on territories without large storage facilities migrated in some years but remained

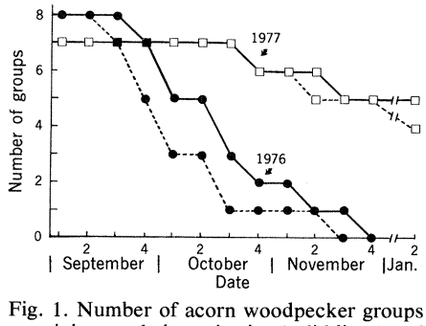

Fig. 1. Number of acorn woodpecker groups remaining on their territories (solid lines) and number of groups with acorn stores, unharvested acorns on oak trees on their territories, or both (dashed lines), during weeks in the fall and early winter of 1976 (N = 8) and 1977 (N = 7). Groups with access to artificial food sources were not included.

resident in others. At the main study site, there was only one resident group during each of the winters between 1974 and 1976. This group had extensive storage facilities and also obtained food from a bird feeder. In 1977–1978, however, seven of the 11 summer breeding territories were still occupied when the study terminated in late March 1978. Most importantly, six of the birds that stayed on their territories were individuals that definitely had left the Research Ranch during the previous winter.

Whether or not a group that occupied a territory without extensive mast storage facilities remained resident during the winter appeared to depend in part upon the number of acorns that were available to the birds in the fall. Acorn production in oaks is extremely variable, not only in different species and during different years but also among individuals of the same species in the same location (*13*). This characteristic made it extremely difficult to obtain reliable estimates of the total number of acorns that were produced on different territories. As an alternative measure of the acorns that were available to the groups, we determined the last date that the members of a group were observed to feed upon acorns. This information was then compared to the last date that the group was seen on its territory. We obtained data for 15 groups on eight different territories during 1976 and 1977. Ten groups left their territories and migrated during the winter. Of these, nine groups were observed on their territories after they had exhausted their acorn supplies, and each group departed from 1 to 2 weeks later. One group left while there were a few acorns on one tree in their territory; however, there was no evidence that this group had any stored acorns.

Figure 1 compares the number of groups that had access to acorns and the number of groups present on their territories during the fall and winter of 1976 and 1977. In 1976, all of the groups had exhausted their acorn stores by the third week in November and all groups had left by the following week. In contrast, during 1977 five groups possessed stores in the last week of November. The same five groups were present in January, and four were still feeding on acorns. These groups remained on their territories until the end of the study in March; at this date they were feeding primarily on flying insects. The major reason for the difference between 1976 and 1977 was that one of the two major species of oak occurring at the Research Ranch, *Quercus arizonica*, produced a larger crop of

acorns in 1977, and it also fruited at a later date.

These data indicate that in years when the oaks produce many acorns, some summer groups on territories without extensive storage facilities are able to store enough acorns to provide food during the winter. These birds are then able to remain resident. Juveniles (and possibly additional adults) may stay on these territories and participate in the utilization and defense of the acorn stores. This in turn may lead to the establishment of stable social groups. In other years, when the mast crop is poor, the limited stores are quickly consumed and the birds are forced to migrate. Thus the acorn woodpecker in this area appears to be able to shift between two different strategies, depending upon the local abundance of a single food resource.

The plasticity of the birds at the Research Ranch may be an evolutionary adaptation to the marginal characteristics of the habitat in this area. During most years the oaks on many territories do not produce sufficient acorns to permit resident groups to become permanently established. During the summer, however, acorn woodpeckers utilize other resources, primarily insects, in addition to acorns (*14*). The Research Ranch is suitable habitat for this species during reproduction, and these birds have the option of moving elsewhere when mast crops are poor (*15*). By migrating during the winter, the woodpeckers can occupy breeding habitat that otherwise would be unsuitable. Selection should favor birds that store acorns and remain resident when conditions permit, because stores are a reliable source of food during the winter and the risks of migration are avoided. Since groups appear to be more efficient than individuals at harvesting and defending mast stores (*12*), selection should also favor individuals that are capable of shifting their behavior to the highly cooperative social organization characteristic of this species in other parts of its range.

The extent to which animals are "locked" into a particular type of social organization by genetic predispositions has attracted considerable interest and controversy (*16*). The results of this study point to the potential dangers of categorizing species or even subspecies in terms of a single social system. The acorn woodpecker has been studied extensively since the 1920's (*17*), but to our knowledge no real suggestion of social plasticity emerged. We have found that acorn woodpeckers at the Research Ranch can follow two entirely different and almost opposite strategies. In one strategy, the birds do not invest time or energy to make acorn storage trees, they migrate during the winter, and they exhibit an essentially asocial type of organization in which the only group is a temporary reproductive pair. The other strategy is characterized by cooperative behavior and by long-term bonds among individuals. Groups construct large storage facilities, collectively utilize and defend the acorn stores, are permanent residents, and breed communally. We have found that both patterns of behavior can occur within the same population and that individual woodpeckers may be able to shift between these strategies in response to different ecological conditions.

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8. H. Swarth [*Pac. Coast Avifauna* **4**, 14 (1904)], in a study of the avifauna of the Huachuca Mountains, said of the acorn woodpecker, "I saw but two or three during February and the early part of March, about the middle of March they began to arrive in numbers, and by April 1 were most abundant."
9. Many of these behavioral characteristics are illustrated by the history during 1976 of the confluence group on the main study area. This group contained an adult male and adult female and fledged three young on 24 August (all birds were banded). One of the juveniles disappeared on 15 September. The rest of the group remained on the territory until 6 October, when the adult male left. A second juvenile departed approximately 16 October. The remaining juvenile and the female did not disappear until more than a week later, on 23 October. A transient adult male temporarily joined these birds on the territory before they left. This male remained on this territory by himself for a week after the female and juvenile departed.
10. These species include the red-headed woodpecker, *Melanerpes erythrocephalus* [L. Kilham, *Auk* **94**, 231 (1977)] and the Lewis's woodpecker *Melanerpes lewis* [C. Bock, *Univ. Calif. Berkeley Publ. Zool.* **92**, 1 (1971)].
11. Resident groups with storage trees were located in Carr Canyon in the Huachuca Mountains and Madera Canyon in the Santa Rita Mountains, west of the study area.
12. The importance of storage facilities for the creation and defense of acorn stores and the relationship between storage behavior and social organization in the acorn woodpecker will be discussed [P. Stacey and C. Bock (in preparation)]; see also MacRoberts and MacRoberts (*1*).
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Endoplasmic Reticulum Sequesters Calcium in the Squid Giant Axon

Abstract. *Axons were loaded with calcium, rapidly frozen, and freeze-substituted. The endoplasmic reticulum, in addition to mitochondria, contained calcium deposits, as indicated by electron probe x-ray microanalysis. Oxalate injected into living axons helped to preserve calcium-containing deposits during preparation for microscopy. It is concluded that the endoplasmic reticulum is a calcium-sequestering compartment in the squid giant axon.*

A variety of cell functions are now known to be regulated by cytoplasmic calcium. The best-known example is control of muscle contraction (*1*); others include actin-myosin interactions leading to motility in nonmuscle cells (*2*), secretion of neurotransmitters and hormones (*3*), control of membrane permeability to other ions (*4, 5*), and processes dependent on polymerization or function of microtubules, or both (*6*). For all of these functions to be under precise control in appropriate regions of each cell and responsive to appropriate stimuli, control of the cytoplasmic free calcium concentration is of critical importance. Studies in a variety of systems have shown that calcium is controlled by a number of co-

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