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FOOD HABITS AND SOCIAL ORGANIZATION OF ACORN WOODPECKERS IN COLOMBIA[1]

GUSTAVO KATTAN
Department of Zoology, University of Florida, Gainesville, FL 32611

Abstract. Colombian populations of Acorn Woodpeckers (*Melanerpes formicivorus flavigula*) inhabit the Andes and are geographically isolated from Central American populations. Their diverse food habits include acorns from *Quercus humboldtii*, the only oak in the Colombian Andes. Unlike birds from North America, however, Colombian Acorn Woodpeckers do not store acorns or rely heavily upon them. Instead, they feed on insects, sap, and fruit year-round. Although oak woodlands seem to be their preferred habitat, Colombian Acorn Woodpeckers are found residing permanently and breeding cooperatively in other kinds of habitat. The limited availability of storage facilities (habitat saturation hypothesis) does not seem to be adequate to explain cooperative breeding in these populations.

Key words: *Acorn Woodpecker; cooperative breeding; habitat saturation; Colombia;* Quercus humboldtii.

INTRODUCTION

The habitat saturation hypothesis is central to some current thinking on the evolution of cooperative breeding in birds (Emlen 1984). This hypothesis suggests that cooperative breeding is a last-resort strategy, adopted by individuals that face very high costs if they attempt to disperse and reproduce on their own (Koenig and Pitelka 1981). The high costs of dispersal and independent reproduction result from specialization or dependence on a localized resource, which makes marginal habitats so inferior in quality as to be unsuitable for sustaining a floating population. The spatially limited nature of the resource leads to saturation of optimal habitat by established individuals; consequently, juveniles have very low chances of territory or resource acquisition, and are ecologically "forced" to remain in their natal territories and wait for a reproductive opening (Koenig and Pitelka 1981, Emlen 1982).

The habitat saturation hypothesis has been invoked to account for cooperative breeding in Acorn Woodpeckers, *Melanerpes formicivorus* (Stacey 1979; Koenig 1981a, 1981b; Koenig and Pitelka 1981). Acorn Woodpeckers live in groups of up to 15 individuals, resident in mixed-oak woodlands throughout the southwestern United States, Central America, and Colombia (MacRoberts and MacRoberts 1976, Short 1982). Koenig (1981a) and Koenig and Pitelka (1981) have suggested that acorn storage facilities, or granaries, are the limiting resource for Acorn Woodpeckers. Each group maintains in its territory several specially modified trees or granaries in which they store acorns (MacRoberts and MacRoberts 1976). In the temperate zone the social structure of Acorn Woodpeckers apparently depends on their ability to store sufficient acorns to provide food for the winter. Bock and Bock (1974) found a correlation between number of oak species and abundance and distribution of Acorn Woodpeckers. A high number of oak species increases the probability of finding sufficient acorns, even in the case of a crop failure in any given species. The occurrence of communal breeding correlates with acorn crop reliability and habitat saturation. In areas with a high number of oak species, Acorn Woodpeckers are resident, groups are large, habitat is saturated, and the birds breed communally. With decreasing numbers of oak species and crop reliability, habitat saturation disappears and the woodpeckers change to a strategy of winter migration and reproduction in pairs (MacRoberts and MacRoberts 1976, Stacey and Bock 1978, Stacey 1979, Trail 1980).

The wide latitudinal distribution and the variety of environments occupied by Acorn Woodpeckers makes a comparative study of interest. In Colombia, the woodpeckers represent a distinct subspecies (*Melanerpes formicivorus flavigula*), with several unique plumage characteris-

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tics (Short 1982). They inhabit the Andes at elevations between 1,500 and 3,500 m, and are isolated from the Central American populations, which reach only western Panama (Short 1982). The existence of only one species of oak in Colombia (*Quercus humboldtii*) makes it unlikely that the woodpeckers depend heavily on acorns as a food resource. The diverse food habits of these birds (MacRoberts 1970, Stacey 1981) and the absence of strong seasonality suggest that Acorn Woodpeckers in Colombia should not be limited by an ecological constraint of the kind they find in the temperate zone. Therefore, they should not exhibit cooperative breeding. In this paper I report on the foraging behavior, social organization, and habitat of Acorn Woodpeckers in Colombia, and point out that habitat saturation may not be sufficient to explain cooperative breeding in these populations.

STUDY AREA AND METHODS

Between November 1982 and June 1983 I made observations of Acorn Woodpeckers at Finca Merenberg, a privately owned reserve located at 2,300 m in the Cordillera Central of Colombia (Fig. 1). The Instituto Geográfico Agustín Codazzi (1977) classifies the region as lower montane wet forest. There are two annual peaks of rainfall (April and November) with precipitation levels of about 190 mm. December and January are dry months with precipitation levels below 50 mm. Mean monthly temperature is 15°C yearround. The topography of this region is characterized by steep slopes and small valleys. Extensive areas have been cleared for pastureland in the valleys and plateaus. Finca Merenberg has about 150 ha of pastures divided by forest corridors which comprise another 150 ha. Primary cloud forest remains on the steepest slopes. A significant portion of the forests are "robledales," homogeneous associations of the oak *Quercus humboldtii*. These robledales have a closed canopy at 20 to 30 m, a clear understory, and very few other species of trees (IGAC 1977).

I located and mapped the territories of 10 groups of Acorn Woodpeckers in Finca Merenberg. Four focal groups were selected for intensive observations (3 days per group per month) and irregular observations were made on the other groups for 3 days more each month.

Following Stacey (1981), I divided foraging behavior into four categories: (1) flycatching, (2) gleaning for insects on trunks and epiphytes, (3) feeding on sap, and (4) eating fruits. Instead of using feeding bouts, however, I recorded the time allocated to each foraging behavior and expressed it as the percentage of total feeding time. Activities were recorded by following individuals as much as possible. Frequently I could observe simultaneously several individuals engaged in the same activity (e.g., flycatching) and in this case I considered them as individual samples, i.e., I multiplied the observation time by the number of individuals and added the result to the total observation time. Time budgets were averaged across all individuals month by month.

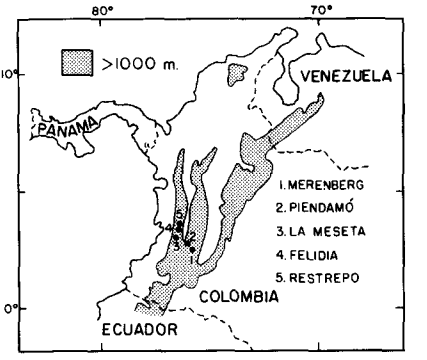

FIGURE 1. Map of Colombia showing the location of Finca Merenberg and other Andean localities with resident populations of Acorn Woodpeckers.

RESULTS

TERRITORIES AND AGGRESSIVE INTERACTIONS

Figure 2 shows the territories of 10 groups of Acorn Woodpeckers at Finca Merenberg. A typical territory included a pasture with scattered trees and a small area of forest. Some territories contained large areas of forest with relatively large gaps. Birds in these territories were active at the gap edges and emergent trees. The woodpeckers used trees in pastures as flycatching and resting perches. Roost and nest holes were in dead trunks isolated in pastures. Woodpecker territories were absent from large areas of Finca Merenberg and surrounding areas that physiognomically resembled the occupied areas. Members of the resident groups occasionally wandered through these otherwise unoccupied areas. Except for these occasional forays, the woodpeckers were always found in their all-purpose territories.

Group size in Finca Merenberg varied from five to more than 10 individuals. The compo-

TABLE 1. Composition of four groups of Acorn Woodpeckers at Finca Merenberg.

Group	Males*	Females	Banded
Planada	5	2	6
Lagunas	6	3	none
Empalizada	6	2	none
La Maria	7	2	none

* Some may be juveniles, which show male plumage in woodpeckers (Short 1982).

sition of the four focal groups is summarized in Table 1. Groups were very cohesive and most members usually carried on their activities together. The *waka* vocalization (MacRoberts and MacRoberts 1976) was continuously given when two or more individuals were in close proximity. Intragroup aggression was seldom observed, and consisted of one individual displacing another at a feeding site.

Groups of Acorn Woodpeckers defended their territories against conspecific intruders. Some territorial boundaries were indefinite because of the presence of dense forest, and most interactions occurred at activity centers for the resident group, such as flycatching perches or sap trees. When an intruder approached, one or more resident birds chased it away, usually giving the *karrit-cut* vocalization (MacRoberts and MacRoberts 1976).

Defense against heterospecifics was not as vigorous and generalized as described by MacRoberts (1970) in California. The woodpeckers tolerated some heterospecific intruders without any apparent interaction. When feeding at fruiting trees, the woodpeckers frequently joined mixed flocks that included quetzals (*Pharomachrus antisianus* and *P. auriceps*) and Emerald Toucanets (*Aulacorhynchus prasinus*). I observed Spot-crowned Woodcreepers (*Lepidocolaptes affinis*) gleaning for insects at sap trees, and Buff-tailed Coronets (*Boissoneaua flavescens*) establishing territories and feeding on sap (Kattan and Murcia 1985), without any aggressive response from the woodpeckers. In contrast, Green Jays (*Cyanocorax yncas*) and Crimson-mantled Woodpeckers (*Piculus rivolii*) that intruded at sap trees were vigorously attacked. I never observed Crimson-mantled Woodpeckers feeding on sap, but they could potentially do it. I do not know the reason for aggression towards Green Jays. Oaks bearing acorns were defended against squirrels (*Sciurus granatensis*). Usually the squirrel retired to feed in dense foliage, where the woodpeckers could not reach it.

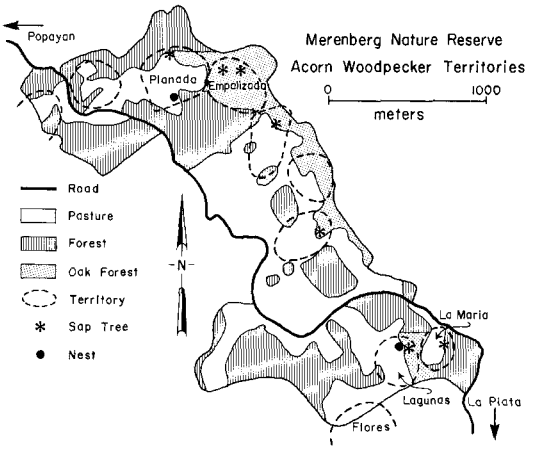

FIGURE 2. Map of Finca Merenberg showing Acorn Woodpecker territories.

FORAGING BEHAVIOR

As in other areas of their range (MacRoberts 1970, Stacey 1981), food habits of Acorn Woodpeckers in Colombia were very diverse and opportunistic. Their diet included mainly insects, sap, and fruits, but they also consumed other foods.

Sap. One of the most important group activities for Acorn Woodpeckers in Finca Merenberg was feeding on sap. This activity was restricted to oaks and all groups had one or two trees used as sap sources in their territories. Usually several or all members of a group spent prolonged periods of time (>1 hr) together feeding on sap. The woodpeckers moved up and down and around the branches, probing holes without any apparent order.

Sap was a major food source for all groups, accounting for approximately 40% of the feeding time during the dry season (January and February). The time spent feeding on sap decreased to 20% in two groups (Planada and Lagunas) while these were feeding young in March and April, and increased again in May and June (Fig. 3). Group Empalizada abandoned two sap trees in March, and due to topographical difficulties I could not record their activities in this period. They resumed the use of one sap tree in April. The sap tree of group La María was cut down in

early March, and by the end of June the birds had not selected a new sap tree.

Flycatching. Acorn Woodpeckers are proficient flycatchers (Stacey 1981), and hawking for insects accounted for approximately 30% of feeding time for groups Planada and Lagunas (Fig. 3) in the dry season. Each group had several preferred hawking perches, such as trunks of dead trees or exposed branches of trees in pastures or forest borders. Captured insects were eaten in "anvils" (MacRoberts 1970), usually the flat surface in the extreme of a truncated branch.

Like feeding on sap, flycatching was frequently a group activity. Most members of the group engaged in flycatching sessions that lasted up to 1 hr. These sessions were probably related to insect swarms and were most frequent at dusk, when the group congregated near the roost cavity. Some captured insects were cached in anvils or bark crevices and retrieved the next morning. Similar congregations for flycatching in Belize are described by Stacey (1981).

During March and April, groups Planada and Lagunas were feeding young and the importance of insects in their diets increased. Flycatching accounted for 40% of feeding time during those days. This percentage declined when the fledglings started to visit sap trees.

Gleaning. Insects also were obtained by thoroughly searching on trunks and branches at all heights, under loose bark, and in epiphyte mats. This foraging mode occurred most frequently on trees along forest edges, and although the woodpecker groups were rather loose when engaged in this activity, most members of the group were within my field of sight and frequently vocalized, presumably to maintain contact. During the dry season, groups Planada and Lagunas gleaned 14% of the feeding time. This proportion increased to about 30% during the nesting season, and decreased again after fledglings attained feeding independence (Fig. 3).

Fruits. Acorn Woodpeckers at Finca Merenberg consumed a wide variety of fleshy fruits. Frugivory was less of a group activity than flycatching or feeding on sap, and I frequently observed woodpeckers feeding on fruits individually. Small fruits were consumed in situ, but large fruits were usually taken to an anvil. A succession of fruiting trees provided a continuous supply for all groups in Finca Merenberg throughout the study. Frugivory accounted for less than 10% of foraging time (Fig. 3).

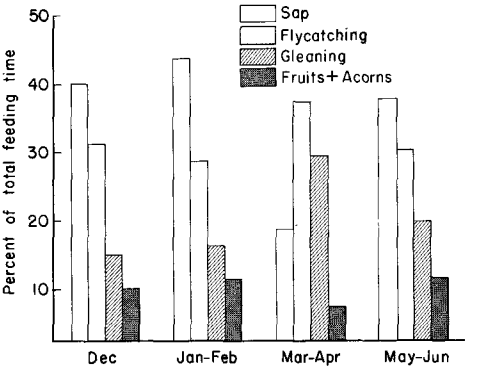

FIGURE 3. Foraging-time budgets for two groups of Acorn Woodpeckers (Planada and Lagunas) at Finca Merenberg.

Acorn consumption was rare and is included in the frugivory category. Oaks at Finca Merenberg usually flower in the dry season (December and January) and fruit at the beginning of the wet season (Günther Büch, pers. comm.). In 1983, the acorn crop failed and few acorns were available to the woodpeckers (pers. observ.). Crop failure is a common occurrence in species of *Quercus* and prevents Acorn Woodpeckers from residing permanently in areas of low oak diversity (Bock and Bock 1974). In Colombia the woodpeckers probably do not rely on acorns as a major food source, and despite the 1983 crop failure, the birds did not abandon their territories. In a 1-year study of the avifauna of Finca Merenberg, Ridgely and Gaulin (1980) did not observe Acorn Woodpeckers feeding on acorns.

Other foraging modes. Acorn Woodpeckers foraged in several rarely observed modes. These included searching on the ground (presumably for insects, possibly for grit), foliage gleaning, eating oak flower catkins, boring on dead trunks, robbing flower nectar, and eating corn in neighboring plantations. I frequently observed woodpeckers boring wood at Finca Merenberg and other localities, but actual extraction of a larva was observed only on three occasions. Boring for insect larvae has not been reported for any other population.

Feeding on flower nectar was observed in two groups. During December 1982, at least six woodpeckers in group Flores (Fig. 2) fed in two trees of *Spirotheca* sp. (Bombacaceae), a species with large buds (10 cm long × 2 cm diameter). The woodpeckers pierced the buds at the base

and fed on the abundant nectar. A large number of flowers was available and members of this group spent about 30% of their foraging time feeding at the flowers. At another locality in the western Andes (Felidia, 1,500 m elevation; Fig. 1), I observed a group of seven woodpeckers in May 1983 feeding on nectar from buds and mature flowers of *Ochroma lagopus* (Bombacaceae).

FOOD STORING

I did not observe any massive or long-term food storing, nor did I find evidence of storing in previous years in Finca Merenberg or in any other of several Colombian localities in which I have observed Acorn Woodpeckers (Fig. 1). The woodpeckers have been observed storing corn and other small seeds in fence post cracks (unpubl. observ. by local ornithologists), but it is not known to what extent the birds rely on this as a long-term food source. I frequently observed short-term storing of insects and fruits, a common behavior for Acorn Woodpeckers (Short 1982). Many of the insects caught in the late-afternoon flycatching sessions were cached overnight. Large fruits and acorns were seldom eaten entirely, but remains were stored in anvils or bromeliads. Retrieval was done by the same or another individual, usually within a few hours. On two occasions I observed individuals harvesting several small fruits and hoarding them in a bromeliad.

BREEDING

Nesting was observed in groups Planada and Lagunas at Finca Merenberg. All members in both groups participated in reproductive activities, such as excavation of the nest cavity, incubation, and feeding of nestlings. Both groups began excavating two nest holes each in early February in dead trees isolated in pastures. After a few days one of the holes was abandoned and the birds continued working on the other one. During the excavation period members of the group actively interacted, chasing one another and vocalizing.

Incubation began in early March, with individuals relaying on average every 7 min (range 1–25), and almost never leaving the nest unattended for more than 5 min. Nests were inaccessible and I could not get information on number of eggs. On 14 March feeding trips to the nest began. While one individual brooded young the other members brought food. The group frequently congregated around the nest and birds hawked for insects from nearby perches.

On 17 April one fledgling was being fed by group Planada but adults were still making feeding trips to the nest. The following day trips to the nest ceased; only one fledgling survived and it was fed by three banded adults (two males and one female), while the rest of the group was rather dispersed. Also in group Lagunas only one young fledged and by late April it was being fed by at least four adult birds. Young in both groups were fed with insects and fruits and they began visiting sap trees in mid-June.

DISCUSSION

Despite the diversity of habitats occupied by Acorn Woodpeckers throughout their latitudinal range, both their social organization and foraging behavior are similar in populations studied to date. Where habitats are suitable for year-round residency, Acorn Woodpeckers live in groups in permanent, all-purpose territories and breed communally. One striking feature of their behavior is the diversity of foods they consume. Differences in proportional use of foraging modes between populations probably reflect seasonal changes in resources and differences between habitats. In the temperate zone the food habits of these woodpeckers are determined mainly by seasonal availability. Sap is a major food source during the spring, insects during the summer, and acorns during fall and winter (MacRoberts 1970). But in the tropical areas of their distribution, the birds use simultaneously several food sources. Stacey (1981) studied foraging behavior of Acorn Woodpeckers during a dry season in Belize and found that the woodpeckers fed on insects in 65% of the foraging bouts observed. Prey was obtained in three different modes: flycatching, gleaning, and probing. The woodpeckers also fed on sap (18% of total foraging bouts), stored acorns (16%), and other rarely used foods such as termites and leaf buds.

Flycatching seems to be the most important foraging mode in Costa Rica (Skutch 1969) and Colombia (Finca Merenberg and other localities; this study). But at Finca Merenberg several food sources were available simultaneously throughout the study, and probably year-round. Sap seems to be a very important food source for this population, especially during nonbreeding sea-

son. Although Skutch (1969) does not report sap feeding in Costa Rica, it presumably occurs throughout the woodpeckers' range, apparently restricted to oaks.

Throughout Central America Acorn Woodpeckers seem to be restricted to oak habitats, and acorn storing has been reported in several countries (Panama, Eisenmann 1946; Guatemala, Skutch 1969; Belize, Stacey 1981). The fact that other food sources are simultaneously available in these populations suggests that food storing is not related to periods of food scarcity. Stacey (1981) suggests that it may be an energetically advantageous behavior, i.e., individuals gain enough energy from the stores to compensate for the expenditure. In Belize, the woodpeckers were feeding on stored acorns when no acorns were present on the oaks, which suggests that the advantage may be to maintain this food source available after the crop has passed.

The long-term storing behavior common in temperate populations seems to be absent in Colombian populations. Miller (1963) reports acorn stores in the San Antonio summit in western Colombia (2,000 m elevation, 15 km west of Cali), but no oaks are present in this region (pers. observ.) and probably Miller did not find an acorn store, but simply a dead tree full of holes. I have not observed acorn storing in any of several localities where I have observed resident Acorn Woodpeckers since 1981 (Fig. 1).

Besides the apparent lack of food-storing behavior in Colombian populations of Acorn Woodpeckers, a major difference with temperate zone populations is found in the habitats they occupy. Although in Colombia the woodpeckers occur in association with oak forests, they are not restricted to this type of habitat. They are also found in sites where oaks are entirely absent. Figure 1 shows some localities where I have made irregular observations of Acorn Woodpeckers since 1981. The habitat at La Meseta, Farallones de Cali (2,000 m elevation), in the western Andes, is similar to that at Finca Merenberg with extensive areas of cloud forest still preserved. Here Acorn Woodpeckers were observed in association with oaks in areas cleared for road construction. Groups of woodpeckers were observed feeding on sap and flycatching. Piendamó (1,800 m), in the Cordillera Central, is a drier habitat with extensive grasslands and only small patches of second growth forest. I observed here a group of more than five woodpeckers in a patch of degraded oak forest; most trees were small, the canopy had large clearings, and the understory was dense. Oaks are absent from the Felidia and Restrepo sites (both at 1,500 m) in the Cordillera Occidental. These areas are primarily farmlands mixed with gardens and shrub habitats, with virtually no forests. Large groups (> five members) of Acorn Woodpeckers are permanently found in both sites.

In summary, semiopen habitats such as farmlands and pasturelands with scattered trees and patches of forest seem to be suitable for Acorn Woodpeckers in the Colombian Andes, and the presence of oaks, although apparently preferred by the birds, is not a requisite for establishing a permanent territory. The woodpeckers also have been observed breeding cooperatively in these oakless sites. I observed a group of seven birds nesting in Felidia in May and June 1983. All members of the group participated in excavation of the nest hole and incubation. I did not follow this nest through fledgling, but the group has resided in the same territory and bred cooperatively for several years (José I. Borrero, pers. comm.).

There is no evidence that Acorn Woodpeckers in Colombia are constrained by a habitat specialization and reliance in acorn storage facilities as they are in the temperate zone. The birds occupy a diversity of habitats, where they are probably not constrained by periods of food scarcity, and seasonality in food availability can be ameliorated by the plasticity of their food habits. Acorns are not a reliable food source and granaries are not necessary. Without the constraints that produce a steep optimal-to-marginal habitat gradient (Koenig and Pitelka 1981), dispersing individuals would be able to find habitats along a gradual quality gradient, habitats where survival and even reproduction would be possible. These results are not in agreement with the hypothesis that cooperative breeding in Colombian Acorn Woodpeckers is forced by lack of habitat suitable for sustaining a floating population.

At this point I do not know what are the proximate factors providing the selective basis for communal breeding in Colombian Acorn Woodpeckers. Elucidating this requires detailed long-term studies of group and population structure and dynamics. Dependence on limited acorn storage facilities does not seem to be adequate to account for communal breeding in these populations.

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