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THE IMPLICATIONS OF GERMINATING ACORNS IN THE GRANARIES OF ACORN WOODPECKERS IN PANAMA¹

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The granary is a central feature in the social organization of Acorn Woodpeckers, *Melanerpes formicivorus* (MacRoberts and MacRoberts 1976, Stacey and Koenig 1984). Groups studied in North America (MacRoberts and MacRoberts 1976, Koenig and Williams 1979) and Belize (Stacey 1981) store ripe acorns on breeding territories for consumption during periods of food scarcity. Granaries of better-studied northern groups average about 1,000–2,000 holes and the extraordinary maximum of 30,000 holes has been reported for some granaries (Stacey and Koenig 1984). Large granaries are maintained by groups of breeding and nonbreeding adult Acorn Woodpeckers that share in the maintenance and consumption of stored acorns.

My observations in Panama of short acorn-storage time, germinating acorns, and oak seedlings in Acorn Woodpecker granaries indicate that acorns represent a perishable and, hence, less dependable stored food source in this part of the woodpecker's range. If group size is related to the maintenance of granaries, then Panamanian Acorn Woodpeckers are expected to occur in smaller groups in a habitat where stored acorns are reduced in importance.

STUDY AREA AND METHODS

I visited the highlands of Chiriqui Province (9° N) in Western Panama during 8–14 August, 6–9 October, and 23–29 December of 1984 and observed Acorn Woodpeckers at four localities. Three sites ranged from east to west on the slopes of Volcán Barú: Finca Menendez, 7.5 km NW Boquete, 1,800 m elevation (visited during October and December); a coffee finca, 2 km SE Bambito, 1,850 m elevation (August, Decem-

ber); Finca Fernandez, 4 km E Cerro Punta, 2,100 m elevation (August, December). The fourth site was on the southern slope of the Cordillera Central near the Costa Rican border: Finca Gonzalo-Batista, 5 km NW Santa Clara, 1,600 m elevation (December). All four sites were open hillside habitats characterized by standing and recumbent trunks of dead oaks (*Quercus* spp.). The Bambito site had 3-m-tall coffee plants spaced in rows whereas the other three sites were sheep or cattle pastures. Mature black oaks occurred individually or in small clumps in the open areas and bordering forest patches.

Six white oak species and three black oak species occurred in the Chiriqui Highlands (Muller 1960). Residents considered "roble," the local name for oaks, common in the area. Panamanian oaks fruited annually (Muller 1960) although crop size may have fluctuated from year to year (R. O'Neal, pers. comm.). In the Boquete area, acorns ripened between mid-July and November (R. O'Neal, pers. comm.), a period of high rainfall (Direccion de Estadística y Censo 1981 y 1982). Unlike North American acorns, those of Panamanian oaks (Fig. 1a) did not appear to undergo a period of dormancy since I found newly sprouted seedlings in the moist litter beneath acorn-bearing trees in October.

I searched pastures systematically for granaries where greatest woodpecker activity occurred because groups studied elsewhere tended to center their activities near storage trees (MacRoberts and MacRoberts 1976, Roberts 1979, Trail 1980). At each granary, I counted the number of holes present in the main storage tree, the number of acorns and seedlings in holes or cracks and crevices of the storage tree, and the number of acorns and seedlings in the cracks and crevices of fence posts and fallen tree trunks within 20 m of the main storage tree. Group size was determined to be the largest number of woodpeckers seen simultaneously in the vicinity of the granary. For a few groups, it was possible to count members as they emerged from the roosting tree. The foraging activities of Acorn Woodpeckers away from granaries were noted whenever possible.

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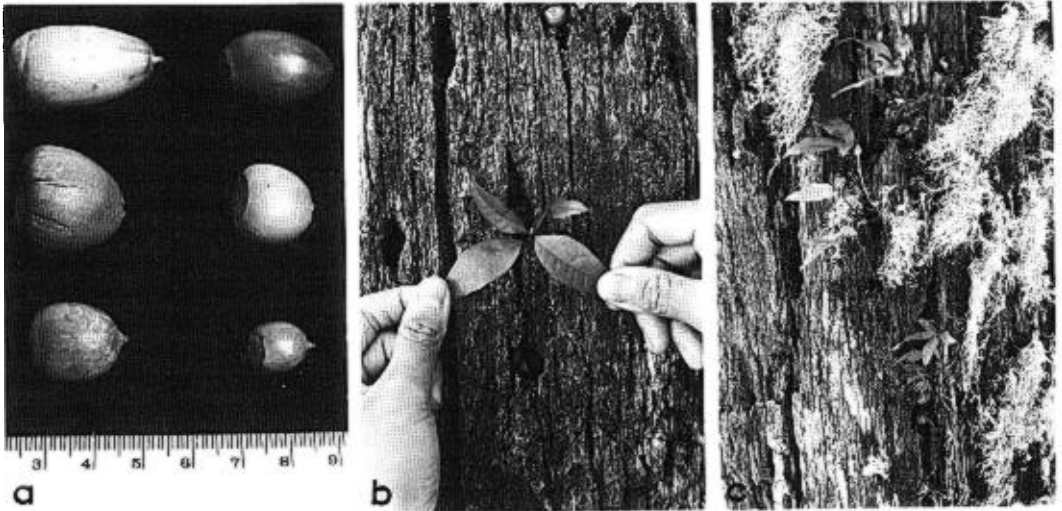


FIGURE 1. (a) Acorns collected from granaries on Fincas Gonzalo-Batista and Finca Menendez; scale in mm. Oak seedlings in (b) woodpecker-made hole and (c) natural cracks and crevices of granary on Finca Menendez.

RESULTS

Eleven Acorn Woodpecker groups were observed with a mean group size of 2.9 individuals (± 0.94 SE). Only the five groups living at Finca Menendez and Finca Gonzalo-Batista maintained granaries (Table 1). Group 2 on Finca Menendez had the largest granary with 850 storage holes of which only 631 were filled with either acorns or seedlings. In October, when woodpeckers were still actively storing, germinating acorns and oak seedlings were already present in the granaries (Fig. 1b, c). By the end of December, only bits of acorns and

oak seedlings remained in the granaries at Finca Menendez.

DISCUSSION

On some days during the northern winter, stored acorns may be the only food eaten by Acorn Woodpeckers (MacRoberts and MacRoberts 1976). Groups which have exhausted their acorn stores during the winter because of low oak density on their territories or because of a poor acorn crop usually abandon their breeding territories and become locally or even extensively

TABLE 1. Group size and granary characteristics of Acorn Woodpeckers in the Chiriqui Highlands of Panama. Percent germination for total number of stored acorns in parentheses.

Locality/group	Group size	No. storage holes	No. intact acorns		No. seedlings and germinated acorns	
			October	December	October	December
Menendez						
Group 1	3	570	530	0	40 (7)	40 (7)
Group 2	2	850	520	0	111 (18)	159 (25)
Group 3	4	550	520	0	6 (1)	12 (2)
Coffee						
Group 4	2	NGP ^a				
Group 5	4	NGP				
Fernandez						
Group 6	2	NGP				
Group 7	3	NGP				
Group 8	4	NGP				
Group 9	2	NGP				
Gonzalo-Batista						
Group 10	2	490		153		23 (15)
Group 11 ^b	4	400		?		?

^a No granary present.

^b Height and angle of storage branch precluded acorn count.

migratory (MacRoberts and MacRoberts 1976, Stacey and Bock 1978, Stacey 1979).

The lack of dormancy in Panamanian acorns suggests that acorn storing cannot be as important in the economy of Panamanian Acorn Woodpeckers as it is for northern populations. If the pattern of acorn storage I observed in Chiriqui during 1984 is typical (Table 1), then the storage efforts of Panamanian woodpeckers only extend acorn availability beyond the fruiting period by 1 month at most. The small number of acorns stored and their rapid depletion on Finca Menendez may have simply reflected local woodpecker response in a year of unusually low acorn production. However, the generally smaller number of storage holes in Panamanian granaries as compared with northern granaries is consistent with the reduced reliability of stored acorns. Eisenmann (1946) provides the only other observation of acorn storing in Panama, but he did not report the number of storage holes or number of stored acorns.

Despite the absence of substantial acorn stores, both storing and nonstoring groups of Acorn Woodpeckers appear to be year-round residents in Chiriqui (A. Fernandez and A. Rivera, pers. comm.). In December, when the oaks on Finca Menendez had dropped all acorns and granaries only contained oak seedlings, no Acorn Woodpeckers were observed feeding on acorns. Individuals observed during this visit were either fly catching or foraging on the ground. Clearly, Panamanian Acorn Woodpeckers have alternative food sources when acorns are no longer available.

The largest groups I observed in Chiriqui had only four Acorn Woodpeckers (Table 1). Wetmore (1968) also only reports having seen them in "pairs and little groups." In contrast, Acorn Woodpecker groups studied in California average four to five individuals and may range up to 15 individuals (MacRoberts and MacRoberts 1976). Koenig (1981) found that per capita reproductive success declined with increasing group size in this cooperatively breeding species. He hypothesized that large groups nonetheless persist because "helpers" are willing to incur the reproductive disadvantages of group living to gain access to group-defended granaries during food-scarce winter months. In Panama, rapid germination of stored acorns and the existence of alternative foods when acorns become scarce may obviate the selective advantage of maintaining granaries and the selective pressure for living in groups larger than pairs. The smaller group size of Acorn Woodpeckers I observed in Chiriqui is consistent with Koenig's hypothesis. Acorn Woodpeckers in neighboring Costa Rica breed from early April through August (Skutch 1969) so that the small groups I observed in Chiriqui may have been nuclear family groups. I did not learn to age the birds until my December trip so I cannot say with confidence that the small groups I observed earlier consisted of parents and young of the year.

Skutch (1969) "looked in vain" for evidence of acorn storage in Costa Rica but observed four of five Acorn Woodpeckers in a group sharing incubation at a nest. In Colombia, where Acorn Woodpeckers did not store

acorns and rarely consumed them, Kattan (1988) observed cooperative breeding in groups that consisted of five to more than 10 individuals. Clearly, Panamanian Acorn Woodpeckers need to be studied in greater detail to determine if small group size is typical and whether cooperative breeding also occurs in this portion of the species' range.

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