ORNITOLOGÍA NEOTROPICAL
(2018) 29: 241–246
ORIGINAL ARTICLE

SOCIAL ORGANIZATION AND FOOD HABITS OF THE ACORN WOODPECKER (*MELANERPES FORMICIVORUS*) IN THE NEOTROPICS INCLUDING OBSERVATIONS IN CENTRAL HONDURAS

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Abstract · Acorn Woodpeckers (*Melanerpes formicivorus*) have been widely studied in North America, mainly due to their complex social system. As a resident bird, Acorn Woodpeckers in much of North America hoard acorns for use during the winter and following spring. The importance of this resource, along with geographic differences in the woodpecker's ecology, has not been as widely studied elsewhere in its range, which extends all the way through Middle America to northern Colombia. This review summarizes published research from five different countries and adds information gathered for a new locality, central Honduras. The results show a gradual change in the importance of acorn storage and a greater variety of foraging behaviors, but with little or no change in social organization. The review highlights the many geographical voids and the need for more thorough studies in most locations to further understand the variation in social and foraging behaviors present throughout this bird's wide geographical range.

Resumen · Organización social y hábitos alimenticios del Carpintero Bellotero (*Melanerpes formicivorus*) en el Neotrópico incluyendo observaciones del centro de Honduras
El Carpintero Bellotero (*Melanerpes formicivorus*) ha sido ampliamente estudiado en Norteamérica, principalmente debido a su complejo sistema social. Como ave residente, el Carpintero Bellotero en gran parte de Norteamérica acumula bellotas de roble para utilizarlas durante el invierno, y la primavera siguiente. La importancia de este recurso, junto con las diferencias geográficas en la ecología del Carpintero Bellotero, no han sido estudiadas tan ampliamente en el resto de su rango que se extiende a lo largo de Centroamérica hasta el norte de Colombia. Esta revisión resume resultados de investigaciones publicadas de cinco países diferentes y agrega información recopilada para una nueva localidad, el centro de Honduras. Los resultados muestran una diferencia gradual en la importancia del almacenamiento de bellotas y una gran variedad de comportamientos de forrajeo, pero patrones similares en la organización social. La revisión resalta los grandes vacíos geográficos y la necesidad de estudios más exhaustivos en la mayoría de las localidades en orden de comprender las variaciones en comportamiento social y de forrajeo presentes en el amplio rango de esta ave.

Key words: Acorn storage · Communal breeding · Foraging behavior · Honduras · *Quercus* · Resource defense

INTRODUCTION

The Acorn Woodpecker (*Melanerpes formicivorus*) is a medium-sized bird of 20–24 centimeters in length and approximately 85 grams of weight (Howell & Webb 1995, Stiles & Skutch 2005) that differs from most other woodpecker species in foraging behavior by storing food items individually in holes drilled in living or dead trees, and in sociality by living in communal groups composed of individuals of both sexes and all ages that share and defend an all-purpose territory (MacRoberts & MacRoberts 1976). It is a common resident of oak forest and pine-oak woodlands, ranging from the Pacific coast of the United States through Middle America to the northern Andes in Colombia. All known populations are dependent on oak forests, with the apparent exception of the Colombian subspecies (*M. f. flavigula*), which has been reported to occur at sites lacking oaks (Kattan 1988).

The Nearctic populations of the Acorn Woodpecker have been widely studied, especially in California (Koenig & Walters 2014) and New Mexico (Stacey 1979, Stacey & Ligon 1987). However, these populations correspond only to two (*M. f. bairdi* and *M. f. formicivorus,* respectively) of the seven subspecies proposed by Benítez-Díaz (1993), five of which are generally of limited geographical distribution and exclusive to Latin America (*M. f. angustifrons, M. f. albeolus, M. f. lineatus, M. f. striatipectus*, and *M. f. flavigula)*. Little is known about the subspecies outside of the USA.

The Acorn Woodpecker is an interesting study subject due to its social and hoarding behaviors, the latter an uncommon feature in tropical birds (Stacey 1981). In Latin America, the earliest observations of Acorn Woodpeckers were primarily made

Receipt 6 February 2018 · First decision 18 April 2018 · Acceptance 13 September 2018 · Online publication 19 September 2018
Communicated by Joseph Wunderle

for bird guides (Peck 1921, Dickey & Van Rossen 1938, Ridgely & Gaulin 1980, Peck 1921, Russell 1964). No attempts were made to thoroughly study their hoarding behavior or their communal living, with the exception of Skutch (1969). Later studies have focused on particular aspects of Acorn Woodpecker ecology, based mainly on observations on the food habits and social organization ranging from a few days to a year. Observational studies have been widely spread both geographically and temporally with seven studies over the last four decades (Koenig & Williams 1979, Stacey 1981, Kattan 1988, Stanback 1989, Wong 1989, Rosas-Espinoza et al. 2008, Flores 2017).

We first present a brief summary of Acorn Woodpecker data from the United States, gathered for comparison with data obtained from a comprehensive bibliographical search of scientific articles dealing with the Acorn Woodpecker's social organization, food habits, and acorn-storage behavior outside the United States. In reviewing the available literature, we assessed the quantitative data of group composition, foraging behavior, and acorn storage holes. However, the data are scarce and studies differ methodologically, making a systematic analysis impractical. Here we present a synthetic review of the most interesting features of the Acorn Woodpecker in the Neotropics focusing on comparisons with temperate populations. We also discuss the proposed hypotheses regarding the communal living and hoarding behavior, and highlight the gaps in Acorn Woodpecker knowledge that need to be filled in order to tackle more complex distribution-wide studies.

OVERVIEW OF ACORN WOODPECKER NEARCTIC POPULATIONS

The Acorn Woodpecker exhibits a complex social structure (Stacey 1979, Koenig 1981), with individuals found in pairs (Stacey & Bock 1978), or establishing permanent family groups up to 15 members (MacRoberts & MacRoberts 1976). The groups exhibit a social system known as communal breeding, which consists of three factions: male coalitions, female coalitions, and nonbreeding helpers-at-the-nest (Koenig et al. 1995, Koenig & Walters 2014).

As highly cooperative birds, all Acorn Woodpecker family members carry out breeding and nurturing activities (Skutch 1961, MacRoberts & MacRoberts 1976, Kattan 1988) and assist in the construction and defense of storage holes, as well as the hoarding of oak acorns (Gutiérrez & Koenig 1978, Sherry 1985, Koenig & Walters 2014). These dried oak fruits are collected and stored during autumn, and then eaten throughout the winter and into the following spring, when they may be fed to nestlings and fledglings (MacRoberts 1970, MacRoberts & MacRoberts 1976, Gutiérrez & Koenig 1978, Sherry 1985, Koenig & Knops 2005). They have also been reported to use immature and mature green fruits that are consumed immediately (MacRoberts 1970).

Groups defend exclusive trees or other structures for acorn storage, normally termed "granaries" (Stacey 1979), which are used collectively and provide an important food source, essential for survival in the winter and subsequent reproductive success (MacRoberts 1970, MacRoberts & MacRoberts 1976, Sherry 1985). Groups show migratory behavior by abandoning their territories when resources are depleted, mainly due to a local failure of the acorn crop (MacRoberts & MacRoberts 1976, Stacey & Bock 1978).

Even though acorn consumption is an important food source for Acorn Woodpeckers, they are also well skilled in catching insects during flight. Insect-foraging behavior, primarily flycatching, increases while rearing chicks and when insects are abundant the woodpeckers may store them (MacRoberts & MacRoberts 1976). The third major food source is oak sap (MacRoberts 1970). Each group territory contains sap trees in which the woodpeckers drill small holes to extract sap in a fashion similar to sapsuckers. Additional but rare foraging behaviors reported for Nearctic populations are gleaning, eating oat seeds, oak catkins (perhaps leaf buds and pistils; MacRoberts & MacRoberts 1976), piñon nuts (Stacey & Jasman 1977), walnuts (Roberts 1979), and other fruits, and depredating lizards (MacRoberts 1970).

ACORN WOODPECKER NEOTROPICAL POPULATIONS

Reported group size from the seven Neotropical studies ranged from two to ten members, similar values to those found in Nearctic populations (Table 1), and with the same components (Koenig et al. 1995). Supporting the assertion that Neotropical Acorn Woodpeckers are organized in three components are observations of multiple adults in groups (Kattan 1988, Stanback 1989); a report of egg removal and consumption by a female of the same group (Flores 2017), typical of the competition faced by females when laying eggs communally (Koenig et al. 1995); and the large number of juveniles, with bigger groups regularly having three to four young per year (Rosas-Espinoza et al. 2008, Flores 2017). Unfortunately, temperate-tropical comparisons of Acorn Woodpecker demography necessary to understand selective pressures favoring communal groups are limited given the absence of studies on juvenile survival rates and population dynamics outside of the USA.

Breeding. In tropical areas, the avian breeding season is considered to occur during the months of March to September (Skutch 1950, Stiles & Skutch 2007). Acorn Woodpecker studies showed similar patterns, with breeding occurring between early March (Russell 1964, Kattan 1988) and mid-June (Russell 1964, Rosas-Espinoza et al. 2008, Flores 2017), but breeding has also been reported to occur in August (Skutch 1969, Flores 2017). This resembles the bimodal breeding season reported for Californian Acorn Woodpeckers, which consists of one main peak in spring (early April and late June) and a second lesser one in autumn, starting in August and extending as late as early November. However, autumn nesting takes place irregularly, in years with larger acorn crops and with warmer summer temperatures (Koenig & Stahl 2007). Therefore, we might expect the equivalent of autumn nesting in Neotropical populations to occur with more regularity.

The excavation of new nest cavities can start one or two months before breeding (Kattan 1988). All group members participate in reproductive tasks (Skutch 1969, Kattan 1988). Hatchlings are mostly fed with insects (Skutch 1969, Kattan 1988) but they can also be fed with acorns, if available. Once the young are fledged and leave the cavity they can be fed by other group members for at least three weeks. The young

Table 1. Comparison of group sizes and acorn storage behavior of the Acorn Woodpecker's (*Melanerpes formicivorus*) Nearctic and Neotropical populations. Data for Neotropical population-group sizes were obtained from the description of groups on each paper. *The data for California was derived from Appendix II of MacRoberts & MacRoberts (1976). **The value assessed belong only to the storage holes measured on *Pinus engelmani*. † Flores (2017) presents a group size before and after breeding for the five focal groups, we used both values to obtain the range and calculate the mean.

Country		Mean	Range	Mean ± SD / range	Source
United States	Oregon	4.25	2–8	3,561.5 ± 2560	Fortner 1979
	California*	6.6	2–18	Not reported	MacRoberts & MacRoberts 1976
				2,900 ± 850	Guitiérrez & Koenig 1978
	Arizona	3.7	2–6	1,418 ± 1,606**	Trail 1980
				Not reported, migratory population	Stacey & Bock 1978
Mexico		5.8	2–10	1,267 ± 1,427	Rosas - Espinoza et al. 2008
Belize		4.75	2–6	20—160	Stacey 1981
Honduras		7.9 †	5–11	391 ± 262.3	Flores 2017
Costa Rica		5.25	3–8	Not reported	Stanback 1989
Panama		2.9	3–4	473	Wong 1989
Colombia		8	5–10	Not reported	Kattan 1988

can be seen pecking bark pieces and leaves during this period (Flores pers. observ.).

SIMILARITIES AND DIFFERENCES IN FORAGING BEHAVIOR IN NEOTROPICAL POPULATIONS

Food habits appear to be similar throughout the Acorn Woodpeckers Neotropical range, although with some variation in terms of relative importance (Table 2). The order of importance of the main foraging behaviors was determined from studies in Mexico (Rosas-Espinoza et al. 2008), Belize (Stacey 1981), and Colombia (Kattan 1988). We excluded the results from Honduras (Flores 2017), since those observations were made only during the acorn-production season.

In contrast to Nearctic populations where acorn hoarding is the main foraging behavior, in its Neotropical range, main behaviors are flycatching, sapsucking, and gleaning**.** Flycatching is especially important in tropical latitudes, given the more constant availability of insects throughout the year, with a high peak during the rainy season.

Sap-feeding seems to be seasonal (Kattan 1988). Even though sap-feeding has been considered apparently restricted to oaks (Kattan 1988), Acorn Woodpeckers have also been observed using other tree species for sapsucking, including nance (*Byrsonima crassifolia*), sweetgum (*Liquidambar styraciflua*), Australian pine (*Casuarina equisetifolia*), pink poui (*Tabebuia rosae*), and an additional unidentified species (Flores 2017). Flores (2017) suggests that this behavior is influenced by the low number of oak trees present in the woodpecker's territory, leading them to increase the diversity of sap sources. The use of sap from other tree species seems to enable birds to persist in acorn depleted territories, thereby making use of the available resources while still visiting other areas in search of acorns.

As with flycatching, gleaning activity increases during the breeding season (Kattan 1988). Recent observations revealed that while gleaning, the birds might capture and manipulate butterfly larvae (Flores 2017) by rubbing them against tree bark (Figure 1) in order to eliminate the numerous urticating's hairs which function as a defense against predators (Payne 1997), or smashing cryptic larvae, possibly to remove the head capsule and skin and gain access to the nutritional content inside (Payne 1997). Given the prominent availability of insects in the Neotropics, this may lead the Acorn Woodpecker to broaden the ways it captures insects. These behaviors might not have been reported earlier due to the relatively little focus on this species' foraging activities in the Neotropics.

Acorn consumption. Acorn consumption did not appear to be such an important resource for Acorn Woodpeckers in Belize (Stacey 1981) and especially in Colombia (Kattan 1988). Even though Colombian populations were found to be correlated with the distribution of the only native oak species (*Quercus humboldtii*), at the local level they can be found in areas without oak or, if coinciding, they may make little use of them as a food source. This suggests that other factors account for their local presence (Freeman & Mason 2015).

More recent investigations in Mexico (Rosas-Espinoza et al. 2008) and Honduras (Flores 2017) demonstrate that immature and mature acorns remain important in the diet of the Acorn Woodpecker outside of North America. Mature acorns are mostly stored, while immature acorns are manipulated on anvils for immediate consumption, similar to Nearctic populations. MacRoberts & MacRoberts (1976) describe anvils as "special locations on the upper surface of horizontal, or nearly horizontal limbs where cracks and crevices provide a suitable hold-fast."

Acorn storage. As in North America, Neotropical Acorn Woodpeckers store acorns in granaries (Koenig & Williams 1979, Stacey 1981, Wong 1989, Rosas-Espinoza et al. 2008, Flores 2017), but they also make greater use of bark crevices (Skutch 1969) and epiphytic plants to store acorns (Stacey 1981, Kattan 1988, Flores 2017). Storage in epiphytic plants is particularly interesting, since bromeliads normally accumulate water, which woodpeckers sometimes drink, and acorns may rot if stored there (Flores pers. observ.), calling into question the efficiency of this storage method.

Even though Neotropical populations have alternative food sources, some Acorn Woodpecker populations still in-

Figure 1. Acorn Woodpeckers (*Melanerpes formicivorus lineatus*) foraging on lepidopteran larvae. A) Adult with a hairy caterpillar on its beak, B) rubbing it against the bark, 13 January 2016, Parque Naciones Unidas (photographs by Stefany Flores) and C) A juvenile holding a cryptic caterpillar that a female had previously manipulated, 8 July 2016, Parque Naciones Unidas (photograph by Víctor Bocanegra).

vest significant energy in storing acorns. This allows them to extend the period of acorn availability and to monopolize consumption of acorns. However, there are locations where the evidence of granary use has not been reported, including Costa Rica (Skutch 1969, Stanback 1989), and in Colombia (Table 1). Colombian populations were found to store acorns only in anvils and bromeliads (Kattan 1988).

Granary selection. Granary selection in the Neotropics seems to be specialized as in the Nearctic populations, with Acorn Woodpecker preferring larger trees (Flores 2017) and also dead trees (Koenig and Williams 1979, Rosas-Espinoza et al. 2008). The preference for larger trees is most likely due to the larger surface area available for food storage (Gutiérrez & Koenig 1978). Moreover, having the food centralized in one place makes it easier for it to be maintained and defended.

Dead trees are usually rotten, which makes them easier targets for the construction of granaries, as well as for roosting and nesting cavities (Gutiérrez & Koenig 1978). Acorn Woodpeckers frequently use pine trees as granaries, however they can also use oak snags or dead branches, especially when pines are absent (Koenig & Williams 1979).

Other food sources. Acorn Woodpeckers forage in a variety of ways that have previously been reported to occur in temperate zones. The major differences in the Neotropics being an increase in ground foraging (Stanback 1989), boring (Kattan 1988), and probing. They also have been observed to consume of ants, termites, and leaf buds (Stacey, 1981).

In Honduras, Acorn Woodpeckers were also observed to store small stones or gravel in (acorn) storage holes, among bark crevices, or even in bromeliads (Flores 2017). The behavior of collecting and storing stones has been previously reported from northern populations, which is interesting because it seems to have no obvious benefit for the birds (Ritter 1921). Koenig (pers. comm.) speculates that this action could be carried out by juveniles as a way of learning about the way in which acorns should be stored, or due to lack of knowledge regarding the appropriate items to store.

Resource defense. Even though their defensive interactions are not as vigorous as reported in temperate zones (MacRoberts 1970), Acorn Woodpeckers still exhibit defensive behavior against individuals of other species (birds and small mammals) that approach their granaries, roosts, anvils,

Table 2. Foraging time budget of the Acorn Woodpecker (*Melanerpes formicivorus*) in four localities from North America to Colombia. For Mexico and Colombia, the method used was time spent carrying out a given behavior, meanwhile in Belize it was bouts. *For the United States the information is only presented as ranks **Gleaning was reported to be seldom observed by MacRoberts & MacRoberts (1976). † The percentages of each foraging behavior were averaged from monthly data. ‡ Kattan (1988) reported <10 % of fruit consumption in general, not specifying acorns, but mentioning that its use was rare.

Location	Foraging behavior					Obs. time (hours)	Obs. period	Reference
	Flycatching	Sap	Gleaning	Acorn	Others			
United States*	2nd	3rd	**	1st			3 years	MacRoberts & MacRoberts 1976
Mexico†	25.1	27.2	14.7	33		416	13 months	Rosas - Espinoza et al. 2008
Belize	19	18	31	16	16	240	2 months	Stacey 1981
Colombia†	35	30	27	‡			7 months	Kattan 1988

sapsucking trees, oak trees, or any other source of food, and even against conspecific belonging to other families (Kattan 1988, Flores 2017). Some birds were found to tolerate some heterospecific intruders (Kattan 1988) or showed reduced defensive behaviors (Flores 2017). This difference may be a consequence of greater competition pressures in Nearctic populations.

CONCLUSIONS

Both major life history features of the Acorn Woodpecker - social organization and foraging behavior - are relatively invariant throughout its Neotropical distribution. Within the Nearctic populations, most variation in group size can be found in California where the largest groups have been reported (Table 1). Stacey (1979) suggested that smaller-sized groups found in New Mexico were the result of higher dispersal rates. This fits with the habitat saturation hypothesis, which holds that dispersal increases because the system is less saturated and individuals have higher possibilities of finding a suitable and available space for reproduction, instead of remaining with their group for consecutive seasons. However, this hypothesis still needs to be tested by systematically comparing the behavior in several different environments with varying levels of saturation (Stacey 1979).

Acorn Woodpeckers' foraging behavior is similar across their range. However, the foraging types show differences on their proportional use between populations, which could reflect seasonal changes in resources and differences between habitats (Kattan 1988). In Nearctic populations, food habits are determined mainly by seasonal availability, but in the Neotropics, where environmental conditions are more stable, Acorn Woodpeckers use alternative food sources, some of them probably year-round. As a result, in the Neotropics some food sources have increased in importance, as is the case for insect consumption, which encompasses other foraging behaviors like gleaning, as well as boring and probing.

Acorn storage remains important in locations across Latin America, even though there is no winter season, and other sources are available throughout the year. However, there is a reduction in the number of acorns that can be stored (Table 1) and consumed, and in the number of granaries, where even within the same sites there are groups with no hoarding behavior (Wong 1989). This could be due to the fact that acorns are available over a longer period of time (Koenig & Williams 1979, Rosas-Espinoza et al. 2008), allowing woodpeckers to harvest fruits directly from the oak trees instead of having to store them (Koenig & Williams 1979).

Food storage occurs in many temperate birds (Sherry 1985), but in tropical species it is only practiced by the Acorn Woodpecker and southern populations of Steller's Jay (*Cyanocitta stelleri*) that store nuts (Stacey 1981). Acorn storage and protection has been hypothesized to have led to the evolution of communal living in the Acorn Woodpecker (Koenig 1981, Koenig & Pitelka 1981). The fact that temperate and tropical Acorn Woodpecker populations exhibit this behavior strengthens this hypothesis. However, some populations across the Neotropical range report little to no use of acorn storage and presence of granaries (Skutch 1969, Kattan 1988, Stanback 1989) while still exhibiting communal living (Table 1). The reliance on acorn consumption is somewhat consistent with oak (*Quercus*, Fagaceae) diversity, which peaks in Mexico with around 161 species (Valencia 2004) and decreases until reaching its southern limit in Colombia, where only one species, the endemic *Q. humboldtii*, is found. Why the southern populations of the Acorn Woodpecker maintain their social behavior despite low levels of oak diversity would be an interesting study topic.

Studies on Acorn Woodpeckers throughout Latin America remain scarce, and methodological differences make it difficult to compare different sites in a quantitative manner. Behavioral variation across its distribution remains an interesting subject to study, both considering the social nature of the bird and its namesake habit of acorn hoarding. Since hypotheses looking to explain these behaviors have been generated with Nearctic populations in mind (*M. f. bairdi* and *M. f. formicivorus*), it is a novel opportunity to test these hypotheses in the Neotropics, where group behavior persists in much the same way despite the fact that populations are less restricted by acorn availability in the autumn. The most important questions on Acorn Woodpecker social behavior and foraging habits remain unanswered. Future studies should be framed by investigating whether the observed geographic differences are correlated with the genetic divergence of populations, being indicative of some more general

geographical patterns, and to which extent local and temporary conditions impact the species' habitat choice, food selection, or storage behaviour.

ACKNOWLEDGMENTS

We deeply thank Walt Koenig for his invaluable support and all his incessant work improving the manuscript. We also thank Gustavo Kattan and an anonymous reviewer for their punctual comments and recommendations, which considerably improved the manuscript. Finally, we appreciate the editorial work by Joseph Wunderle, Kaspar Delhey, and André Weller.

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