THE SOCIAL SYSTEM OF THE TEXAS GREEN JAY

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ABSTRACT.—Accessory birds were absent at the nests of Green Jays (*Cyanocorax yncas*). However, young stayed in the family flock for one year. After the young from the following year fledged, the 1-yr-old young were forced from their natal territory by the breeding male. These young either dispersed into adjacent habitat or became floaters within their former territories until, possibly, a breeding position opened up in a family flock. The yearlings provided a significant amount of territorial defense, which freed the breeders of much of the energetic costs inflicted on them by the stringent territoriality required in south Texas habitat.

I propose that south Texas Green Jays represent an early stage in the evolutionary sequence of development of cooperative breeding as a response to environmental factors. The retention of young on the natal territory without helping at the nest represents an evolutionary early step, heretofore only hypothesized, that may lead to a more complex cooperative system that includes helpers at the nest. *Received 3 September 1985, accepted 28 January 1986.*

New World Jays possess a wide variety of social organizations and breeding systems that range from territoriality by breeding pairs in the Blue Jay (Cyanocitta cristata; Hardy 1961); through highly cooperative breeding systems in the Gray-breasted (Mexican) Jay (Aphelocoma ultramarina; Brown 1963, 1970), the Tufted Jay (Cyanocorax dickeyi; Crossin 1967), and the Florida Scrub Jay (Aphelocoma coerulescens; Woolfenden 1975); to colonialism in the Pinyon Jay (Gymnorhinus cyanocephalus; Balda and Bateman 1972). The neotropical Green Jay (Cyanocorax yncas) has been most intensively studied in Colombia, South America where it occurs in groups of 3-9 individuals that defend stable territories all year (Alvarez 1975). Breeding is cooperative, with members of the group helping to feed and care for the young. Juvenile Green Jays do not disperse immediately from the parental group but stay as helpers at the nest for a minimum of one additional breeding season.

There is no published information on the social system of the North American population of the Green Jay, which occurs from just north of the Rio Grande River in southeast Texas south to north-central Honduras (Meyer de Schauensee 1966). References to the behavior of the Texas population of Green Jays are anecdotal, and information on breeding biology in North America consists primarily of nest location, height, and composition and clutch size (Merrill 1878, Sennett 1878, Bendire 1895, Sutton et al. 1950).

I report here on detailed field observations of the Green Jay's social system and discuss the evolution of helping behavior and territoriality in the North American population. I also compare the social systems of the two disjunct Green Jay populations.

METHODS AND MATERIALS

I studied Green Jays at Santa Ana National Wildlife Refuge (NWR) located approximately 12 km south of Alamo, Hidalgo Co., Texas on the Rio Grande River. The area is semiarid, with a mean annual rainfall of 45 cm. Most of the precipitation occurs in late spring and early autumn. Autumn precipitation occasionally is enhanced by the movement of a low-pressure center onshore and into the Rio Grande Valley. The mean temperature in winter is 15.5°C, spring 20.5°C, summer 28°C, and autumn 27°C. The lowest recorded temperature is -9°C and the highest 43°C (Fleetwood 1973).

The refuge consists of about 900 ha covered mostly by evergreen, dry subtropical forest. All land adjacent to the refuge has been cleared for agriculture and is subject to intense aerial spraying of insecticides and herbicides. Thus, Santa Ana NWR has been an island of natural habitat for 30-40 yr. The most common trees are elm (*Celtis* spp. and *Ulmus crasi*-

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folia), ebony (Pithecellobium flexicaule), anaqua (Ehretia anacua), mesquite (varieties of Prosopis juliflora), huisache (Acacia farnesiana), and retama (Parkinsonia aculeata). Beneath the canopy is a dense understory of shrubs and thorny vines.

A total of 2,850 h of observations was made from April 1981 through June 1984. I followed three flocks of jays for the majority of time and observed one other flock only occasionally. Hereafter, the study flocks will be referred to as Ray's Group, Handicap Group, Blue Group, and Willow Lake Group. As of March 1984 a total of 133 after-hatching-year (AHY) Green Jays has been banded within the refuge. Each bird received one numbered metal USF&WS band and up to four plastic colored leg bands. The plastic bands were cemented with Duco Cement and none were lost during the study period.

The jays were captured in potter traps baited with bird seed. Each jay was banded, measured, and weighed using a 300-g Pesola spring scale. Each jay was then released within 10 m of the capture point. I sexed Green Jays by mating behavior because I could not discern any sexual differences in plumage, size, or other characteristics. Sexing via laparotomies was not attempted because of Alvarez's (1975) lack of success with this method.

Nine nests were located during the study period, and the majority of time was spent observing nests of Ray's Group and the Handicap Group. Observations commenced when a nest was located and continued until all young fledged. In 1981, 6-h nest observation periods were conducted for Ray's Group after the young had hatched. In 1982 and 1983, 4-h observation periods per nest were conducted and were rotated for the study nests so that observations included some morning and afternoon study periods for all nests until young fledged. After the young fledged, observations continued on a similar rotating basis for 2–3 weeks.

RESULTS

General observations.—Green Jays were conspicuous and scolded loudly during the entire year except for the spring and summer breeding season, when they became secretive and difficult to locate. At this time the adults and young rarely scolded or called when alarmed but, rather, silently moved away.

Adult Green Jays tended to avoid flying in open spaces. In 5 yr of observations, I saw only 5 jays fly 30–200 m in the open, and all 5 were juveniles. Adult Green Jays preferred to fly short distances in dense understory until they arrived at their destination. When flying in the open, Green Jays had an undulating, woodpecker-like flight. The apparent avoidance of flying in the open results in heavy use of travel corridors of dense vegetation.

Three reports on Green Jay age at Santa Ana NWR exist. The first (Kennard 1975) gave the age of an AHY Green Jay banded at Santa Ana NWR as 9 yr, 9 months at death. On 15 June 1982, I live-trapped an AHY jay that was banded on 30 November 1972 at the same location. This bird extended the minimum lifespan to 10 yr, 0 months. This jay, released unharmed, has not been resighted since. Finally, Clapp et al. (1983) discovered a Santa Ana Green Jay record extending the age record to 10 yr, 8 months. These age records were of Green Jays banded and recaptured within the confines of this small refuge. As of late 1985, it was unknown whether a significant number of banded jays had ventured outside of the refuge boundaries. Only one record of dispersal beyond the refuge exists. A female (banded 8 January 1982) was found dead on 24 February 1983 south of Reynosa, Tamaulipas, Mexico, 15 km west of Santa Ana NWR.

Group composition.—In south Texas, Green Jays lived in a family group that remained stable from one breeding season to the end of the next. In the winter and spring a family group consisted of the monogamous breeding adult male and female and all surviving offspring from the previous year's reproductive effort.

During and after the breeding season, the family group size increased by the addition of the young produced during the current year's reproductive effort. At this time the group size peaked. Several weeks after the young fledged, the yearling jays were driven out of their natal territory by the adult breeding male. The family group size was then reduced to just the breeding pair and the current year's young. This group size is maintained until the next breeding season (Figs. 1 and 2, Table 1).

During the winter, the family group usually foraged together (>76%, n = 142). In the spring when the breeding pair was building the nest, laying eggs, etc., the yearlings spent almost all of their time foraging together within the parental territory yet having little contact with the breeders. The breeding male and female foraged within 100 m of the nest during this time (>90%, n = 78). The yearlings joined in a "greeting" behavior with the adult pair in the morning and at dusk before separating.

After the current year's young fledged, the

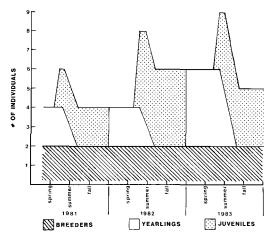


Fig. 1. Composition of Ray's Group study flock, 1981–1983. In the age classification used in this study, by winter those individuals initially placed in the "juvenile" category become "yearlings."

breeding male spent increasing amounts of time with the yearlings foraging and moving about the entire territory and only occasionally rejoined the female during the day. The breeding female foraged alone at this time and provided insect prey for the dependent fledglings without help from other family group members. An increase in agonistic behavior between the breeding male and the yearlings was first noticed 4-10 days after fledging. Eventually, yearlings were banished from the family flock by the breeding male, a process that took 3-5 weeks and sometimes included fighting and grappling between the breeding male and one or more of the yearlings of the family flock. The yearlings usually remained together for 3-6 weeks near the periphery of the natal territory, but avoided the breeding male.

By winter, some yearling jays had dispersed into areas adjacent to their natal territory. It is not known how far they dispersed, but observations revealed that some apparently became floaters and remained close to the area in which they were hatched. In spring 1984, a banded female (hatched by Ray's Group in 1982) was observed feeding three fledglings in the Handicap Group territory, where she had previously been observed alone or with other jays. This suggests that a female can spend at least one year as a floater before being incorporated into a group's breeding structure.

Territorial behavior.-Green Jays in Texas were

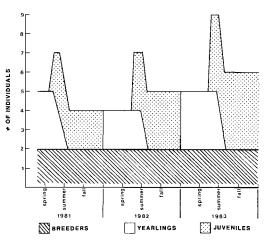


Fig. 2. Composition of Handicap Group study flock, 1981-1983.

territorial year-round, but exhibited a higher degree of territorial defense behavior during the spring and summer breeding season. The territory boundaries were defined through observations of daily group movements and of numerous boundary disputes between adjacent family groups. Territorial boundaries for the four groups usually coincided with topographic features such as lakes, field boundaries, and roads (Fig. 3).

Texas Green Jay territory size averaged 16.2 ha (Table 2). The territories supported 4–9 individuals in a family group as well as one or more other jays that were not family members. The four study flock territories were located in an area of the refuge dominated by mesquite and ebony species, which I consider excellent Green Jay habitat.

Family groups vigorously defended their territories at all times. I observed 27 territorial encounters between Ray's Group and either the Handicap Group or the Blue Group. The encounters lasted from 5.5 min to slightly more than 42 min (mean = 22 min). A typical territorial encounter began when 1-3 intruders flew into a group's territory while calling very loudly. The first member of the family flock to respond, if the intrusion was near the nest area, usually was the breeding male. He would alight on a branch within 0.5 m of the intruder and face the other bird. Both birds would call constantly while performing stereotyped displays characteristic of this territorial behavior (Gayou 1984). Only twice did I observe the breeding

TABLE 1. Green Jay family group composition one week postfledging.^a

	1981		1982			1983		
В	Y	F	В	Y	F	В	Y	F
2	2	2	2	2	4	2	4	3
2	3	2	2	2	3	2	3	4
						2	3	2
			2	2	3	2	3	3
	B 2	B Y 2 2	B Y F 2 2 2 2	B Y F B 2 2 2 2 2 2 3 2 2 2	B Y F B Y 2 2 2 2 2 2 2 3 2 2 2 2	B Y F B Y F 2 2 2 2 2 4	B Y F B Y F B 2 2 2 2 4 2 3 2 2 2 3 2 2 3 2 2 3 2	B Y F B Y F B Y 2 2 2 2 4 2 4 2 3 2 2 2 4 2 4 2 3 2 2 3 2 3 2 3

^a B = breeders, Y = yearlings, F = fledglings.

male face an intruder alone. In all other recorded observations, yearling members of the group whose territory was being invaded also participated in the defense behavior. They exhibited the same calls and postures as the breeding male. The breeding female rarely participated, and usually only if an intruder came near the nest. She normally watched from an adjacent tree, always arrived last at a particular territorial encounter, and was the first to depart. Eventually the intruders broke off the encounter and flew away calling loudly. The breeding male continued to call loudly from the tree tops on the edge of his territory for some minutes after the intruders had left (mean time = 11 min, max = 23 min, n = 22). The yearlings quieted quickly and usually flew away several minutes before the breeding male resumed his prior activities.

In 20 of 31 (65%) territorial encounters among all groups, yearlings detected the intruders first. The breeding pair arrived very quickly if the intrusion was near the nest, but not at all if the event occurred at a distant periphery from the nest area. In two instances I observed yearlings from Ray's Group respond to an incursion by a member of the Willow Lake Group at the southern edge of Willow Lake. The intruder was driven off without the breeding male or female's participation.

In 19 of 27 territorial encounters between Ray's Group and the other groups, all calling and displaying occurred in and around one open area where territories of three study flocks met. Whether this area was consistently used as a display arena for territorial encounters is unknown, but these preliminary observations suggest that Green Jays preferred to display in open areas during these encounters. I have never observed a territorial encounter in dense vegetation.

A solitary floater jay was pursued outside of

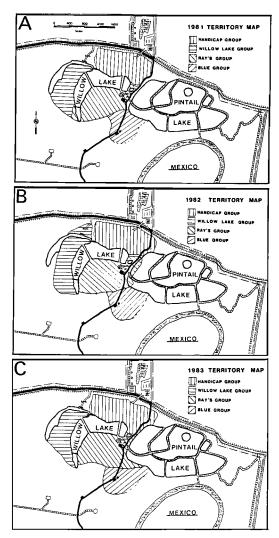


Fig. 3. Territory maps of study groups in (A) 1981, (B) 1982, and (C) 1983. The eastern territory boundaries for the Blue Group could not be determined precisely because of dense brush and are represented by dashed lines.

a territory only if it made itself conspicuous by calling frequently or perching near a family group member. At this time the floater was chased without the typical territorial encounter display behavior because the floater did not respond and withdrew immediately. Generally, floaters foraged in a particular territory without being chased if they remained inconspicuous and quiet.

Although territories are defended yearround, vigorous territorial defense became ev-

	1981	1982	1983	Mean	
Ray's Group	13.6 (6)	18.6 (8)	15.9 (9)	16.0 (7.7)	
Handicap Group	18.6 (7)	14.9 (7)	15.8 (9)	16.4 (7.7)	
Willow Lake Group	16.1 (?)	16.3 (?)	16.3 (7)	16.2 (7.0)	

TABLE 2. Green Jay family group territory size (ha), 1981-1983. Group sizes are given in parentheses.

ident during March and April. The entire family group joined in maintaining the territorial boundaries. This group behavior involved moving along the territory boundaries while calling loudly. During these family group patrols, especially in the breeding season, there were always several territorial encounters between family groups of adjacent territories that consisted of stereotyped behaviors and calling. After such an encounter, the family group's display behaviors and calling were maintained at a higher level of intensity for a period of time. Family groups were more likely to patrol areas of their territories subject to frequent incursions by other jays. During patrol periods mating behaviors occurred frequently between the breeding male and female. After nesting began, the yearlings continued to move about the group territory and intercept and drive away any intruding jays.

Absence of nest helpers at Green Jay nests.— During approximately 73 h of observing nestlings and fledglings over 4 yr, I observed only the parents feed the young (Gayou 1984). Nine nests were located during the study period, and the majority of time was spent observing nests of Ray's Group and the Handicap Group.

During nesting, the yearling family group members approached the nest only in the morning to call and display with the breeders for several minutes. The yearlings flew off and usually did not return to the nest area until dusk, when there was another short display period. Breeders were never observed to prevent a yearling group member from approaching a nest. Even after the young had fledged and might beg from all family group members during these "greeting" periods, only the breeding female responded. No attempt to bring food to a nest or fledged young by any banded yearling was observed.

DISCUSSION

Based on my observations at the Santa Ana Refuge, Green Jays at the northern limit of their range lack helpers at the nest. In contrast, Green Jays in Colombia have helpers at the nest (Alvarez 1975). The biology of these two populations apparently share several features. The mating behaviors (Gayou 1984) are like the descriptions provided by Alvarez (1975), and various aspects of foraging ecology, mating calls, and reproductive behavior also share many characteristics. Other similarities are apparent in yearly family group stability: the number of family group members in both populations remained constant from one breeding season to the next. Although Alvarez (1975) did not discuss the ultimate fate of the one-year-old Colombian Green Jays at the beginning of the next year's breeding season, he described a system whereby new groups sometimes formed during the current breeding season that enabled young to become members of these new groups. South Texas Green Jays are driven from their parental groups a few weeks after the current year's young have fledged.

The differences that occur are of major significance and provide a divergence between what was previously thought to be identical allopatric populations (Hardy 1961). The most significant difference between the populations is in social systems. South Texas Green Jays have an extended interaction between parents and young but do not employ helpers at the nest during any stage of the reproductive cycle. Colombia Green Jays have a year-round fixed composition flock and utilize helpers at the nest. In addition, breeding Colombian female jays provide a minimal amount of food items once the young are fledged (Alvarez 1975). South Texas breeding females appear to fill the opposite role in caring for the young because they provide almost 100% of the food items for their fledged young (Gayou 1984).

The evolution of group territoriality.—Given that both populations of Green Jays show some degree of group territoriality, I hypothesize that both face some amount of habitat saturation, with the more severe situation occurring in

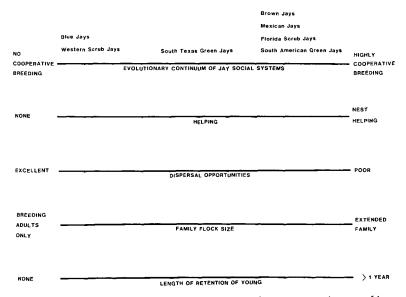


Fig. 4. Hypothetical status of south Texas Green Jays on the evolutionary continuum of jay social systems.

South America. Alvarez (1975) found that C. yncas move in small flocks in a wide variety of habitats ranging from grasslands to dense secondary forests. Each flock is a discrete social unit that defends a stable territory the entire year. The boundaries of the flock territory are defended by all members, and aggression occurs frequently between members of different flocks during territorial encounters. The flocks do not dissolve during the breeding season, and only one pair breeds in each flock. In addition, Alvarez found that a flock of Green Jays may divide to produce two separate flocks with adjacent territories. This behavior seems similar to Florida Scrub Jay territory splitting by related offspring of the parents in a particular territory, and suggests that South American Green Jays may be under similar habitat constraints as Florida Scrub Jays. Yet the question of when group territories evolved for this population remains a matter for speculation. Because South American Green Jays are somewhat dependent on occasional superabundant resources, selection pressures would seem to favor a system whereby a flock could locate temporary resources quickly so as to exploit them to the fullest possible extent (Alvarez 1975). Additional flock members would help a group locate such resources (Krebs et al. 1983). If food in Colombia is less abundant, more patchily distributed, and shows less seasonal variation than in Texas, helpers should increase the ultimate number of young fledged from a nest by being able to locate more food over a given time interval. In fact, flocks with the highest survivorship of fledged young had the most helpers (Alvarez 1975). South American Green Jays also may remain within a flock if the alternative to dispersal will result in a significant increase in mortality. Although Alvarez (1975) presented no data on dispersal or mortality as a result of dispersal, his data indicate an apparently significant trend of young jays to remain within a flock as helpers for at least one, and perhaps several, years. Thus, selection would reinforce the helping aspect of the social system of these jays, but such selection might not occur in south Texas.

The situation appears less extreme in south Texas. There must be some cost to dispersal or young Green Jays would leave sooner, and yearlings must provide some benefit in territorial defense. Yet, south Texas Green Jays seem to be able to disperse into marginal habitat or to become floaters within their former territories. A floater would retain the benefits of its high-quality natal territory and could quickly fill an opening in an adjacent flock as an experienced, older bird if the time between openings in breeding positions in such a saturated habitat were short. Preliminary observations of south Texas Green Jays showed that breeding positions became available in Ray's Group after three years and in the Handicap Group after two years (Gayou 1984).

Because yearling south Texas Green Jays do not provide help directly to siblings, they do not gain breeding experience, their potential social bonds are limited, and they have limited effect on the success of closely related kin. Even so, some trade-off of costs and benefits exists, associated with the territory defense behavior that probably benefits the breeders by freeing them (especially the males) of some of the costs inflicted by the stringent territoriality required in south Texas.

Insufficient information exists on sex ratios to draw conclusions about mate availability as a cause for reducing the amount of dispersal among south Texas jays. A last consideration for dispersal, that of dealing with an unpredictable or harsh environment, is probably not very important for south Texas Green Jays. Observations suggest that the high degree of habitat saturation of jays in south Texas does not change dramatically through the year, as it might in an unpredictable environment. Occasional cold or hurricanes may cause some mortality, but these are rare events.

Evolution of jay social systems. - The social systems employed by various jay species range from the most simple to the most highly cooperative system. It has been hypothesized that at one stage in the evolutionary sequence, the breeders of a particular species began to allow the young to remain within the territory for an additional time period (Brown 1974, 1978; Ricklefs 1975; Gaston 1978; Emlen 1982a, b). Once young were permitted to remain on the natal territory, they developed helping behavior as a method of increasing their overall fitness. They gained reproductive experience, helped raise siblings, located resources, and detected predators. The parents tolerated this behavior because the young could not disperse, perhaps because of the lack of suitable habitat in which to disperse and survive.

I propose that south Texas Green Jays exemplify an early stage in the evolutionary sequence of development of cooperative breeding as one response to environmental factors. Although south Texas Green Jays permit young to remain on a territory even though the young do not act as nest helpers, the territorial defense behavior of the young birds undoubtedly aids the parents reciprocally. Retention of the young in the natal territory without helping at the nest may be an important evolutionary step that leads to a more complex cooperative system that includes helpers at the nest (Fig. 4). Thus, the social system used by south Texas Green Jays represents a first example of this early stage in the evolution of cooperative breeding.

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LITERATURE CITED

- ALVAREZ, H. 1975. The social system of the Green Jay in Colombia. Living Bird 14: 5-44.
- BALDA, R. P., & G. C. BATEMAN. 1972. The breeding biology of the Pinyon Jay. Living Bird 11: 5-42.
- BENDIRE, C. E. 1895. Life histories of North American birds. U.S. Natl. Mus. Spec. Bull. 3.
- BROWN, J. L. 1963. Social organization and behavior of the Mexican Jay. Condor 65: 126-153.
- ——. 1970. Cooperative breeding and altruistic behavior in the Mexican Jay Aphelocoma ultramarina. Anim. Behav. 18: 366-378.
- ——. 1974. Alternative routes to sociality in jays with a theory for the evolution of altruism and communal breeding. Amer. Zool. 14: 63-80.
- ——. 1978. Avian communal breeding systems. Ann. Rev. Ecol. Syst. 9: 421–422.
- CLAPP, R. B., M. K. KLIMKIEWICZ, & A. G. FUTCHER. 1983. Longevity records of North American birds: Columbidae through Paridae. J. Field Ornithol. 54: 123–137.
- CROSSIN, R. S. 1967. The breeding biology of the Tufted Jay. Proc. Western Found. Vert. Zool. 1: 265–297.
- EMLEN, S. T. 1982a. The evolution of helping behavior I. An ecological constraints model. Amer. Natur. 119: 29-39.
- . 1982b. The evolution of helping II. The role of behavioral conflict. Amer. Natur. 119: 40–53.
- FLEETWOOD, R. J. 1973. Plants of Santa Ana National Wildlife Refuge. Washington, D.C., U.S. Dept. Interior, Fish Wildl. Serv.

- GASTON, A. J. 1978. The evolution of group territorial behavior and cooperative breeding. Amer. Natur. 112: 1091–1100.
- GAYOU, D. C. 1984. The behavioral ecology of Texas Green Jays (*Cyanocorax yncas*). Unpublished Ph.D. dissertation, Columbia, Univ. Missouri.
- HARDY, J. W. 1961. Studies in behavior and phylogeny of certain New World jays (Garrulinae). Univ. Kansas Sci. Bull. 42: 13–149.
- KENNARD, J. H. 1975. Longevity records of North American birds. Bird-Banding 456: 55-73.
- KREBS, J. R., D. W. STEPHENS, & W. J. SUTHERLAND. 1983. Perspectives in optimal foraging. Pp. 165– 216 in Perspectives in ornithology (A. H. Brush and G. A. Clark, Jr., Eds.). New York, Cambridge Univ. Press.
- MERRILL, J. C. 1878. Notes on the ornithology of southern Texas, being a list of birds observed in

the vicinity of Fort Brown, Texas, from February 1876 to June 1878. Proc. U.S. Natl. Mus. 1: 118-173.

- MEYER DE SCHAUENSEE, R. 1966. The species of birds of South America and their distribution. Wynnewood, Pennsylvania, Livingston Publ. Co.
- RICKLEFS, R. E. 1975. The evolution of co-operative breeding in birds. Ibis 117: 531-534.
- SENNETT, G. B. 1878. Notes on the ornithology of the lower Rio Grande of Texas from observations made during the season of 1877. Bull. U.S. Geol. Geogr. Surv. Territory 4: 1–66.
- SUTTON, G. M., R. B. LEA, & E. P. EDWARDS. 1950. Notes on the ranges and breeding habits of certain Mexican birds. Bird-Banding 21: 45-59.
- WOOLFENDEN, G. E. 1975. Florida Scrub Jay helpers at the nest. Auk 92: 1-15.