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FLORIDA SCRUB JAY HELPERS AT THE NEST

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THE list of birds for which helpers at the nest commonly occur has grown rapidly since Skutch's (1961) compilation, and now about 80 species in 32 different families are known to exhibit such cooperative breeding (Harrison 1969, Fry 1972). Widespread as the phenomenon may be, few studies have continued long enough to provide much information on the effect helpers have on reproduction or the possible filial relationships of the helpers to the breeders. In the absence of such facts avian cooperative breeding provides little information of use in the current controversy about group or kin selection versus individual selection (Hamilton 1964).

This preliminary report on the helper system of the Florida Scrub Jay, *Aphelocoma c. coerulescens*, is based on 5 years of study, 1969–73, at the Archbold Biological Station in Highlands County, Florida. A recent paper (Woolfenden 1973), which provides information on some aspects of breeding and survival, characterizes Florida Scrub Jays as long-lived, permanently territorial, permanently monogamous, and single brooded with a short, highly synchronized breeding season. The overall stability of the population is indicated by the fact that during the last 3 years of study only about five territories have disappeared and six new ones come into existence in a sample of some 27 territories that occupy a study tract of about 400 ha.

Though they often live near men's dwellings and are easily tamed, only one report of Florida Scrub Jays having helpers existed prior to 1969 (Grimes 1940). Amadon (1944) was aware of Grimes' record, but concluded from his own observations, which perforce were brief, that such aid probably was unusual. The Florida race of *Aphelocoma coerulescens* is a disjunct population of a species that inhabits much of southwestern North America (Pitelka 1951), where the many ornithologists who have

A Scrub Jay male (1G-OS) defends his nest from human intruders, while his mate (1G-PS) perches hesitantly on the rim and their helper male (1G-WS), probably their son, assumes a defensive posture on a nearby branch (see Table 7).

(From a photograph by James N. Layne 9 May 1969; reproduction costs supported by the University of South Florida.)

studied its breeding have never reported a helper (e.g. Hardy 1961, Brown 1963, Stewart et al. 1972, Verbeek 1973). The probable absence of helpers from western populations, and their postulated rarity in Florida 30 years ago could lead one to suspect the phenomenon is either of very recent origin or a feature only of the population at the Archbold Biological Station. Therefore careful scrutiny of Amadon's observations is warranted.

For 1 month at the Archbold Station, Amadon watched mostly unmarked breeding Scrub Jays, concentrating on six pairs, two of which produced nestlings. He saw no birds additional to the pairs feeding young, but he did notice that some jays, even when near a nest, were tolerated by its owners, and that sometimes these presumed nonbreeders begged from the mated male. He also frequently saw noisy groups of squabbling jays, but apparently always at some distance from any nest. My conclusion, based on 5 years of watching marked jays, is that the birds Amadon (1944) studied were behaving as they do today (Woolfenden 1973). The extra birds he saw near some nests were almost certainly accepted family members and therefore potential helpers at the nest, and their begging was an appeasement gesture to the dominant breeding male. The flocks he saw engaged in excited screeching and chasing most likely were family groups embroiled in territorial disputes with other families.

The Scrub Jays at Archbold Staton are not persecuted, and some artificial feeding occurs. At Hicoria, 2 miles south of the station, Florida Scrub Jays also have helpers (Westcott 1970), and these birds, which do not visit the station, are afforded neither extra protection nor artificial food. Thus man's activities apparently have caused no changes in the Florida Scrub Jay social structure.

MARKING METHODS

The case histories of certain helper jays described later are best explained by referring to the color coding system that identifies the individuals. Each jay is ringed with a unique combination of one USFWS metal band and two color bands. All three bands may be on the same leg. The color bands are plastic spirals (purchased from A. C. Hughes in England) sealed with a drop of acetone. The plastic bands become brittle after several years, break, drop off, and must be replaced. Although loss of the service band occurs in Blue Jays, *Cyanocitta cristata* (Bergstrom 1964), this has not occurred with Scrub Jays. The symbols of the 10 different colors are: white (W), red (R), dark green (dG), yellow (Y), dark blue (dB), purple (P), orange (O), light green (lG), light pink (Pi), and light blue (lB). The service band is designated S. With the bird facing the observer the bands are recorded in sequence from top to bottom, left to right. Specifically this means from proximal to distal, right leg first, left leg last. In recording the color code a dash always follows any bands on the right leg and precedes any bands on the left leg. To this date each year class has a unique combination of bands, with two others reserved for

individuals of unknown age. Letting C represent any color, these combinations are: CC-S for birds hatched 1969, -CCS for 1970, CCS- for 1971, CS-C for 1972, and S-CC for 1973, with C-CS and C-SC for birds of unknown age.

The Effect of Florida Scrub Jay Helpers

Florida Scrub Jay helpers participate in territory and nest defense, mobbing predators, and in certain phases of care of the young. They feed nestlings and fledglings, and defend the nest. They also remove fecal sacs. They do not assist in nest building, incubating, or brooding. At least for the last two activities it appears that the breeders discourage participation by the helpers. Normally any bird other than a member of the breeding pair that comes near an active nest prior to hatching is threatened by the breeding female who sits tight and vocally summons her mate, who flies to the nest and chases away the intruder. Rare exceptions exist with older and persistent helpers, and particularly during renesting following loss of nestlings or young fledglings. A persistent helper may even feed the breeding female, a task normally performed only by her mate. The frontispiece depicts a defending helper male.

During the excitement when humans visit nests, some helpers defend so vigorously they replace or even displace a less resolute breeder from the nest. The breeding male then often divides his time between harassing the intruder and threatening his helper. At times three or more members of a family will pile atop each other on the nest and assume defensive attitudes.

The breeders, helpers, and any fledglings they produce are together most of the time as they move through their territory; therefore, inadvertently if not otherwise, helpers also assist the young in learning to forage and avoid predators.

The simplest measure of the role of helpers in reproduction is to calculate breeding success for pairs with helpers versus pairs without helpers for all years combined. A total of 47 complete seasons of breeding (herein often referred to as seasonal breedings) by pairs without helpers resulted in an average per pair of 1.1 fledglings (defined as the first meaning in Van Tyne and Berger 1959: 568) and 0.5 independent young (defined as jays that live to their first August, or about 3 months after fledging), while 59 seasonal breedings by pairs with helpers produced 2.1 fledglings and 1.3 independent young. By these measures one could claim that having helpers enhances Florida Scrub Jay reproduction by a multiple of two or three. The results of each of the five seasons taken separately (Table 1) lend support to this conclusion. Certain biases are incorporated into such computations, for example first breeders, because

TABLE 1

REPRODUCTIVE SUCCESS OF FLORIDA SCRUB JAYS FOR EACH OF FIVE BREEDING SEASONS FOR PAIRS WITHOUT AND WITH HELPERS

Years	Number of pairs		Fledglings per pair ($\bar{x}$)		Independent young per pair ($\bar{x}$)	
	Without H[1]	With H	Without H	With H	Without H	With H
1969	2	5	0	2.6	0	2.0
1970	8	8	2.0	3.5	1.3	1.8
1971	6	19	1.3	2.1	1.0	1.2
1972	13	17	0.3	1.6	0.1	1.1
1973	18	10	1.3	1.8	0.4	1.1

[1] H = helper.

of the species' social organization, virtually never have helpers, lay smaller clutches (Woolfenden 1973) and produce fewer clutches than more experienced jays, and therefore have fewer opportunities for raising young. Fortunately the data are sufficient to make some refinements in the methods of measuring reproduction.

In Table 2 the six seasonal breedings by novice pairs (column A), are separated from pairs in which at least one member is experienced in tending an egg (columns B–E). With the novice breeders deleted, pairs without helpers (column B) still produce significantly fewer offspring than pairs with helpers (columns C–E). Thus the important conclusion that Florida Scrub Jay helpers increase breeding success seems justified.

Further analysis of the data given in Table 2 sheds light on the ways in which helping benefits the bird. The sample of six novice pairs is small, but comparison with those experienced breeders that also lack helpers (column B) shows the former not only tend to lay fewer eggs each season (3.7 vs. 4.9), but also certainly produce far fewer young. The fact that the novices produce only 0.2 nestlings per egg compared with 0.5 for the experienced breeders without helpers indicates that neophytes also are less successful at producing nestlings from their fewer eggs than the experienced breeders are from their larger number of eggs.

Further analysis of reproduction by pairs in which at least one member is experienced reveals that those without helpers (column B) produce almost as many nestlings, but only about half as many older young, as pairs with helpers (columns C–E). These data suggest that an especially critical step in the reproductive process is fledging nestlings. For the same sample of experienced breeders, the number of nestlings produced per egg, the number of fledglings produced per nestling, and the number of independent young produced per fledgling are stable at 0.5 for pairs lacking helpers, while they range higher from 0.6 to 0.8 for pairs with helpers. Ap-

TABLE 2

REPRODUCTIVE SUCCESS OF SCRUB JAYS AS RELATED TO BREEDING EXPERIENCE AND NUMBER OF HELPERS PER PAIR[1]

	Column				
	A	B	C	D	E
Number of seasonal breedings	6	41	26	20	13
Breeding experience	No	Yes	Yes	Yes	Yes
Helpers per pair	0	0	1	2	3–5
Eggs per pair	3.7	4.9	5.1	4.6	4.8
Nestlings per pair	0.8	2.6	2.9	3.1	3.1
Fledglings per pair	0	1.2	2.1	2.2	2.2
Independent young per pair	0	0.6	1.0	1.6	1.7

[1] Student's t was used to test the means in each row after transformation by $\sqrt{x + \frac{1}{2}}$. Column A differs from columns B–E for nestlings and fledglings, and from C–E for independent young. Column B differs from C–E for fledglings and from D–E for independent young. No other means in the same row differ at this level ($P \leq 0.05$).

parently helpers increase the production of independent young, although the help they provide varies for the several stages leading to independency.

Applying the stricter criterion of using only pairs previously successful at fledging young to measure the effect of helpers reduces the sample size to only 26 pairs, but the results are nearly identical to those described for pairs whose minimum experience was that one bird had tended an egg. Successful pairs without helpers produced 1.0 fledglings each during nine seasonal breedings, but with helpers produced 2.0 fledglings during 34 seasonal breedings ($P < 0.2$). Apparently experience beyond one member of the pair having tended eggs is unimportant to successful breeding in the Florida Scrub Jay.

Once a Scrub Jay starts breeding it tends to live in the same territory until it dies (Woolfenden 1973). Furthermore the boundaries of territories occupied by enduring pairs are rather stable. Thus an even more refined measure of how much helpers increase reproduction is to compare breeding success for the same pairs, all previously successful, during years without helpers versus years with helpers. The sample is small, but four pairs whose previous young disappeared as fledglings produced 0.6 fledglings per pair during five seasons without helpers, versus 2.4 fledglings during eight seasons with helpers ($P < 0.1$). The even greater difference in breeding success between these families without versus with helpers as compared to the differences presented above may be the result of small sample sizes. Any difference showing that helpers increase the reproductive success of the same pair in the same territory weakens the argument that territorial quality is the controlling factor and helpers merely

TABLE 3

PRODUCTION OF YEARLINGS, POTENTIAL BREEDERS, AND ACTUAL BREEDERS AS RELATED TO NUMBER OF HELPERS PER PAIR[1]

	Column				
	A	B	C	D	E
Number of seasonal breedings	1	15	15	10	7
Breeding experience	No	Yes	Yes	Yes	Yes
Helpers per pair	0	0	1	2	3–5
Yearlings per pair	0	0.7	0.8	1.2	1.0
Potential breeders per pair	0	0.5	0.8	0.6	1.0
Actual breeders per pair	0	0.2	0.3	0.4	0.9

[1] Student's t was used to test the means in each row after transformation by $\sqrt{x + \frac{1}{2}}$. Column A differs from columns C–E for yearlings, and from D–E for potential breeders. No other means in the same row differ at this level ($P \leq 0.05$).

reflect successful breeding in previous years. If quality of territory were the controlling factor, results closer to parity than the previously obtained one-to-two ratio would be expected but instead they are even farther from it. As the project continues these ideas will be tested with larger samples.

Perhaps the best measure of reproduction is how many new breeders are produced—a difficult measurement in Florida Scrub Jays. First the birds exhibit delayed and variable maturity. Breeding never occurs before age 2, and for some jays not for several more years. Second is the common problem of dispersal. No doubt some marked jays have bred so far away we have not found them.

The problem of variable maturity is lessened by measuring production of 2-year-olds or potential breeders. The problem of dispersal is lessened two ways. First, dispersal is extremely limited in Florida Scrub Jays (Woolfenden 1973), and therefore less critical than might be expected. Second if the assumption is made that dispersal affects families with varying numbers of helpers about equally, then the values can be used at least to measure relative productivity. Table 3 shows the results, based only on birds hatched from 1969 to 1971, and, as before, families without helpers tend to produce fewer birds that those with helpers.

Included in Table 3 are figures showing the production of yearling jays for the same 3-year sample, 1969–71. The results for yearlings probably are more accurate than those for older birds, because virtually all Florida Scrub Jays remain in their natal territories as yearlings.

SOURCE OF HELPERS

Number of helpers.—Of our individually marked Florida Scrub Jays 78 have been helpers or potential helpers. The latter category includes

TABLE 4

PERCENTAGE OF SCRUB JAY PAIRS WITH DIFFERENT NUMBERS OF HELPERS

Year	Number of pairs	Number of helpers						
		1	2	3	4	5	1–5	0
1969	7	57	14	–	–	–	71	29
1970	19	21	11	16	–	–	48	52
1971	31	29	29	6	3	3	70	30
1972	36	22	19	14	–	–	55	45
1973	28	21	11	–	4	–	36	64
All 5	121	26	18	8	2	1	55	45

nonbreeding Scrub Jays that, according to our behavioral observations, would have fed young, and would have been allowed to feed them if nesting had continued past the egg stage.

A total of 121 seasonal breedings by 67 different Scrub Jay pairs have been studied closely enough to determine the number of helpers and potential helpers each pair had during the 5 years. As shown in Table 4 about half of these pairs had helpers, and for those that did, the number ranged from one to five. A direct correlation exists between fledging success one year (Table 1) and the number of pairs with helpers the following year (Table 4). Because of many other factors that affect breeding the reverse is not true; a high percentage of helpers per breeding pair does not insure greater productivity that year than during a year when fewer breeders have helpers.

Age of helpers.—Florida Scrub Jays often help for several years before they become breeders themselves. No 1-year-old ever has shown overt signs of sexual maturity and only 13 of about 34 2-year-olds are known to have bred. Another 21 2-year-olds were known to remain as unmated helpers. Helping seldom continues beyond 3 years. One individual from the 1969-year-class helped in 1973 at age 4, but late in the breeding season it moved elsewhere and paired, therefore probably no birds from the 1969-year-class will help in 1974. One other jay, which hatched in 1968 or earlier, helped in 1973, so helping occurs even at age 5 years, but it is rare. Table 5 gives the age distribution of 77 known-age helpers for three consecutive breeding seasons. Including data from 1971 may bias the sample slightly in favor of younger birds as no known 3-year-olds existed in 1971, but including this year-class probably reduces the chance of a different bias. Breeding success one year obviously affects the number of helpers in years that follow. Breeding success in 1970 was the highest of all 5 years (Table 1) and in 1971 71% of the helpers were yearlings. Breeding success in 1972 was the lowest of the 5 years, while

TABLE 5

THE AGE DISTRIBUTION OF FLORIDA SCRUB JAY HELPERS DURING THREE BREEDING SEASONS

Year	Age of helper in years			
	1	2	3	4
1971	27	7	–[1]	–
1972	17	10	3	–
1973	5	4	3	1
1971–1973 combined	49	21	6	1
Percent of total	64%	27%	8%	1%

[1] A dash signifies no birds of that age possible.

1971 was near average. Thus including these 3 years in Table 5 may show most of the variation typical of the population as well as showing an average typical of the Scrub Jay through the years.

Sex ratios of helpers.—Scrub Jays are difficult to sex by external morphology (Pitelka 1951). Males average larger, never give the emphatic hiccup call (Amadon 1944), and never develop a brood patch; they further reveal their sex by dominating all females in their families (Woolfenden and Fitzpatrick MS). Using these criteria 70 of the 78 Scrub Jay helpers were sexed as follows: definite males 30, probable males 8, definite females 28, and probable females 4. Many of our sex determinations based on behavior have been substantiated later when the birds bred.

The sex ratio for helpers of all ages gives little indication of an imbalance, which is contrary to that in certain other avian helper systems (Rowley 1965, Fry 1972). As virtually all yearling jays help, and yearlings form the bulk of the helpers (Table 5), it is important to investigate sex ratios of helpers of different ages. For 58 yearling helpers the sex ratio is near parity with 26 males, 25 females, and 7 undetermined. The ratio for older helpers shifts to a preponderance of males. Tabulating the sexes of the 40 helpers hatched in 1969 and 1970 reveals this change (Table 6). As mentioned, few Scrub Jays remain helpers beyond age 3

TABLE 6

SEX RATIOS OF THE SAME 40 SCRUB JAY HELPERS DURING 3 CONSECUTIVE YEARS

Age in years	Sex		
	Male	Female	Undetermined
1	18	17	5
2	10	6	1
3	5	0	0

TABLE 7

HISTORY OF TWO SIBLING FLORIDA SCRUB JAYS (YY-S ♂ AND -dGWS ♂) THAT HELP THEIR BROTHER

Year	Birds and their status[1]		History
1969	Breeders:	1G-OS ♂, 1G-PS ♀	Following breeding 1G-WS ♂ begins pairing at the periphery of the territory, then he disappears.
	Helper:	1G-WS ♂	
	Fledglings:	WW-S ♂, YY-S ♂, PiPi-S ?, OO-S ?†	
1970	Breeders:	1G-OS ♂†, 1G-PS ♀†	WW-S ♂, who dominates his brothers, takes over his natal territory when his parents die.
	Helpers:	WW-S ♂, YY-S ♂, PiPi-S ?†	
	Fledglings:	-dGWS ♂, -RWS ?†, -YWS ?†, -dBWS ?†	
1971	Breeders:	WW-S ♂, 1B-OS ♀	1B-OS ♀ immigrates from afar (see Table 9). YY-S ♂ replaces a lost breeder in June in an adjacent territory wherein he now dominates WW-S ♂. YY-S ♂'s mate dies in November, and he returns to his natal territory where he resumes his hierarchal position between his brothers.
	Helpers:	YY-S ♂, -dGWS ♂	
	Fledglings:	None	
1972	Breeders:	WW-S ♂, 1B-OS ♀	-dGWS ♂, who departed in December 1971, pairs, breeds, fails, and then returns home with his mate R-SdG ♀. He feeds his brother's fledglings while his mate is forced to remain at the periphery of the group's activities within the territory.
	Helpers:	YY-S ♂, -dGWS ♂	
	Fledglings:	dBS-R ?†, PS-R ?†, OS-R ?†	
	Visitor:	R-SdG ♀	
1973	Breeders:	WW-S ♂, 1B-OS ♀†	R-SdG ♀ "divorces," returns to the general area where she bred in 1972 and pairs with a previously unmated male. YY-S ♂ departs and breeds elsewhere with a previously unmated female. WW-S ♂ and his mate prevent -dGWS ♂ from feeding their nestlings.
	Helper:	-dGWS ♂	
	Fledglings:	None	
	Breeders:	YY-S ♂, -ROS ♀	

[1] ? = sex unknown, † = died before next breeding season. Two or more breeding pairs listed for the same year always lived in separate territories. See text for methods of color coding individual jays.

(Table 5), but the one 1969 hatchling that helped when 4 years old was a male. Three 1970 hatchlings, that because they did not pair at age 3.4 years may be helpers in 1974, also are males.

Family relationships of helpers.—Of the 78 Scrub Jay helpers 56 are of known parentage, and all but 5 of these have helped only their parents or one parent and a stepparent. Four of the remaining five jays helped only brothers and their mates. The fifth helper (-lGlGS ♂) fed young of a pair neither member of which was related to him, and one additional jay of unknown age and parentage (P-SdG ♂) helped a pair that in all likelihood included no relative. Tables 7, 8, and 9 give brief histories

TABLE 8

HISTORY OF TWO FLORIDA SCRUB JAY BROOD-MATES (1G1GS-♂ AND Pi1GS-♂) THAT HELP THEIR BROTHER

Year	Birds and their status[1]		History
1971	Breeders:	O-dBS♂†, dB-PS♀	The parents of the two unknown-age helpers are not known, but probably they are the two breeders of 1971. All 5 helpers disperse and O-dBS♂ dies during the winter 1971–72.
	Helpers	Pi-dGS♂, Pi-YS♀, OW-S♂, -OdBS♂, -1GdBS♀	
	Fledglings:	1G1GS-♂, Pi1GS-♂	
1972	Breeders:	-ORS♂, dB-PS♀	dB-PS♀ obtains a new mate, -ORS♂, who is very aggressive toward 1G1GS-♂ and Pi1GS-♂; both leave. Pi-dGS♂ pairs with a divorcée as both move into an adjacent territory vacated by the death of both occupants. 1G1GS-♂ and Pi1GS-♂ come to reside here where they feed nestlings of the breeders. A predator takes the young. 1B1B-S♀ divorces again, and Pi-dGS♂ obtains a new mate.
	Helpers:	None	
	Fledgling:	RS-P♂	
	Breeders:	Pi-dGS♂, 1B1B-S♀	
	Helpers:	1G1GS-♂, Pi1GS-♂	
	Fledglings:	None	
1973	Breeders:	-ORS♂, dB-PS♀	
	Helper:	RS-P♂	
	Fledglings:	None	
	Breeders:	Pi-dGS♂, R-SO♀	1G1GS-♂ helps care for two fledglings; Pi1GS-♂ disappears.
	Helper:	1G1GS-♂	
	Fledglings:	S-RW?, S-dGW?†	

[1] See Table 7 for explanation of symbols.

of these six individuals. These tables reveal how the deaths of certain members of a Scrub Jay family can result in a jay's helping breeders other than its parents. These tables list only the jays present in a given territory late in each breeding season and important to the thesis.

DISCUSSION

It seems certain from the preceding analyses of productivity that cooperation between nonbreeders and breeders increases reproductive success in Florida Scrub Jays. Evidence that helpers really do help exists for only one other bird, the Superb Blue Wren, *Malurus cyaneus* (Rowley 1965). The differences Fry (1972) found in nesting success between simple pairs and multiple breeding units for the Red-throated Bee-eater, *Merops bulocki*, were not statistically significant, and Ligon's (1970) sample for Red-cockaded Woodpecker, *Dendrocopos borealis*, breeders with and without helpers is small. Gaston (1973) suspected from his study of cooperative breeding by Long-tailed Tits, *Aegithalos caudatus*, in England that their helpers may not increase productivity. For some

TABLE 9

HISTORY OF TWO FLORIDA SCRUB JAYS (P-SdG ♂ AND -1G1GS ♂) THAT HELP BREEDERS TO WHICH THEY ARE NOT CLOSELY RELATED

Year	Birds and their status[1]		History
1970	Breeders:	R-OS ♂ †, Y-WS ♀	In September R-OS ♂ injures his wing. Soon thereafter 5 jays move into the territory, 3 males including O-PiS ♂ and P-SdG ♂, one female 1B-OS ♀ (see Table 7), and one whose sex was not determined.
	Helper:	dB-YS ♀	
	Fledglings:	-1G1GS ♂, -1B1BS ?†, -PiPiS ?†	
1971	Breeders:	O-PiS ♂, Y-WS ♀	Intruder O-PiS ♂ replaces R-OS ♂ when he dies late in winter. Of the remaining 4 intruders, 3 disperse or disappear, leaving only P-SdG ♂. He and the other 2 nonbreeders help feed nestlings.
	Helpers:	dB-YS ♀, P-SdG ♂, -1G1GS ♂	
	Fledglings:	None	
1972	Breeders:	O-PiS ♂ †, Y-WS ♀ †	The same breeders, with the same 3 helpers, fail again during the nestling stage. During the winter 1972–73 both breeders and the female helper die.
	Helpers:	dB-YS ♀ †, P-SdG ♂, -1G1GS ♂	
	Fledglings:	None	
1973	Breeders:	P-SdG ♂, P-dBS ♀	P-SdG ♂ pairs with a widow from an adjacent territory. They occupy parts of three adjacent, former territories and, with help from -1G1GS ♂, fledge 2 young.
	Helper:	-1G1GS ♂	
	Fledglings:	S-RR ♀, S-NN ?†	

[1] N = no color band; see Table 7 for explanation of other symbols.

birds reasons more important than increasing the production of new young may exist for nonbreeding individuals living with breeders, as is suspected by Zahavi (1974) for the Arabian Babbler, *Turdoides squamiceps*.

Cooperative breeding in the Florida Scrub Jay depends on young remaining in their natal territory, where they help with certain phases of reproduction during the years that follow. Virtually all yearlings and well over half of all 2-year-old Florida Scrub Jays act as helpers, as do some individuals 3 and 4 years of age and perhaps even older. The Scrub Jays of western North America are asocial. They live as pairs in permanent territories from which they drive the young when they reach independency (Verbeek 1973). The congeneric Mexican Jay, *Aphelocoma ultramarina*, lives in flocks that contain about one or two dozen birds, all of which defend one large permanent territory. Usually each flock includes two breeding pairs, and all members of the flock participate in raising the young of both nests (Brown 1963, 1972). If the highly social Mexican Jays descended from asocial ancestors, they may have passed through a stage similar to that exemplified by present-day Florida Scrub Jays.

Although some western Scrub Jays are capable of breeding at 1 year (Pitelka *in* Brown 1963: 151), Florida Scrub Jays never breed before they are 2 years old, and many not until they are 3 or 4. Thus it seems that Florida Scrub Jays exhibit either highly variable physiological maturity or delayed first breeding following maturation. Because some individuals have remained nonbreeders as long as 4 years, and because one known-age 2-year-old nonbreeder had testes as large as breeders (Woolfenden MS), delayed first breeding, controlled by ecological and behavioral factors, seems the better of the two choices. Mexican Jays also do not breed until several years old. Brown (1972) followed three marked birds hatched before 1969 and they remained as nonbreeding members of the same flock through the 1970 breeding. At present no more is known about their maturation. Delayed first breeding also typifies the Superb Blue Wren. Many individuals, mostly males, do not pair, and therefore probably do not breed for several years while others do at age 1 year (Rowley 1965).

Virtually all Florida Scrub Jays live as members of family groups, and families always include only one breeding pair. The sex ratio of yearings is equal, while the older helpers are mostly males. Thus males must outnumber females in the entire population, and this must come about through the males having a longer lifespan. During the 5 years of study sex ratios for all members of from 9 to 37 families ($\bar{x} = 25$) have varied annually from a 7% deficit to a 31% surplus of males. For all 5 years combined, males exceed females by 16%. Preliminary data indicate female jays disperse earlier and farther than males, probably accounting for much of their earlier mortality. Furthermore breeding females may die when slightly younger than their mates. During 196 accumulated bird years 40 breeders have been lost (Woolfenden 1973), of which 21 have been females.

The Superb Blue Wren is nearly identical to the Florida Scrub Jay in sociology, and Rowley (1965, *in* Lack 1968) postulates similar causes for their social organization. Fry (1972) found a preponderance of males in the Red-throated Bee-eater, which is known to have extra males at nests, and also in several other socially breeding Meropidae. It may be that having more males than females is basic to the social organization of many cooperatively breeding birds.

Scrub Jay helpers rarely assist breeders other than their parents or stepparents. From a sample of 56 known-parentage jays that helped with 73 seasonal breedings, only five have been exceptions, and four of these helped their brothers (Tables 7, 8, 9). Characteristics of the jay's habitat and social organization appear to limit opportunities for nonbreeding

birds, which are the potential helpers, from living anywhere but in their natal territory. Habitat acceptable to Florida Scrub Jays is generally scarce and often exists in isolated small patches (Pitelka 1951, Westcott 1970). Herein breeding pairs, often accompanied by offspring from several breeding seasons, remain together throughout the year defending rather large and permanent territories. Normally breeders accept the presence of their own young in their territories, but do not tolerate intrusion by any other individuals. Thus about the only places where young jays can exist are in their natal territories.

The existence of excess males in Florida Scrub Jay populations increases opportunities for mate selection by females. A major variable in the quality of males may be breeding experience, part of which the males accumulate while helping. Males unable to obtain a mate, and with limited opportunities for living anywhere but in their natal territory, by living at home not only increase the productivity of their close relatives, but also may improve their own chances of reproductive success in the future.

The presence of excess males, which results in some remaining as helpers in the same family for several years, appears to lead to an increasingly close relationship between certain helper males and the breeding female. This closeness is expressed by the helper male's participation in such acts as feeding the female prior to and during incubation, which normally are tasks performed only by the breeding male. Copulation, a better measure of mateship than any other behavioral trait, is unfortunately rarely observed in the jays. I have seen it only twice, both times under poor conditions, and once D. Bruce Barbour (pers. comm.) induced it during a playback experiment. Of course even observed copulation does not prove whose sperm is fertilizing the eggs, and this may be extremely critical to the existence of a particular social system. The closeness of certain male-male-female trios in the jays could be viewed as wife-sharing as is described for the Tasmanian Native Hen, *Tribonyx mortierii,* (Maynard Smith and Ridpath 1972), but for the jays at least it seems doubtful that more than one male fertilizes the eggs.

As helpers do enhance the reproductive efforts of breeders, and the breeders that receive their assistance almost invariably are their close relatives, the Florida Scrub Jay is existing under the forces of kin selection. Obviously any young produced are potential genetic competitors of the helpers, but from currently available information it is wrong to conclude the helpers are altruists and receive no benefits from the system. Kin selection need not operate solely on altruism, and the possibility remains that helper jays profit as much or more from the existence of younger members in the same family as do the young themselves.

Florida Scrub Jays have strong drives to exist as members of a group, and this suggests individuals function best when in a group. By enhancing the reproductive efforts of others, helper jays increase the probability they will be members of a group. Florida Scrub Jays of both sexes often live several years past the age of minimum maturity before they become breeders, and this suggests that it is often difficult to obtain a breeding territory. By increasing the size of the group to which they belong, older helpers may be improving their own chances of obtaining space in which to breed. This hypothesis is derived from preliminary analyses of data on family hierarchies and changes in territory size. Fieldwork is being concentrated now on these facets of Scrub Jay demography.

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SUMMARY

About half of the breeders in a marked population of Florida Scrub Jays nest as simple pairs, the others have helpers. Pairs with helpers produce more offspring than those without. Even the same pairs living in the same territory produce more offspring during seasons when helpers are present.

The percentage of breeders with helpers reflects in part breeding success in recent past years, and has varied from 36% to 71%. Virtually all yearling jays help, as do about half the 2-year-olds. Few jays help beyond age 3. The sex ratio of yearling helpers is about 1:1. Older helpers are preponderantly males. The sex ratio of the entire population favors males by about 15%. Females probably die younger because they disperse earlier and farther than males. Furthermore they may suffer a slightly higher death rate as breeders than males. Florida Scrub Jays rarely help any breeders other than their parents or stepparents. The fact that they rarely help any birds other than close relatives fits a prediction of kin selection, but the helpers may not be pure altruists. Indeed, the helpers could well be the major beneficiaries of the social system of Florida Scrub Jays. This possibility is currently under investigation.

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