

DOMINANCE IN THE FLORIDA SCRUB JAY

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Studies of intraspecific dominance abound in the ornithological literature, but relatively few are based on the activities of free-living birds. The study of captive flocks, and even of wild groups attracted to feeding stations, may severely limit opportunities for discovering functions of dominance behavior in birds. Despite these limitations, several recent reports that in certain birds dominance is closely related to territoriality are convincing (Brown 1963, Dixon 1965, Wiley 1973, Smith 1976). More commonplace hypotheses relate dominance to differential allocation of limited food supplies (Wynne-Edwards 1962, Lack 1966: 284), though this relationship seems difficult to demonstrate in the field (despite Fretwell 1969).

Florida Scrub Jays (*Aphelocoma c. coerulescens*) typically rear a single brood annually during a brief breeding season (Woolfenden 1973). Surviving offspring normally remain with their parents for at least one year during which they assist them in breeding (Woolfenden 1975). Eventually many of these helpers establish themselves as breeders either by replacing lost breeders of neighboring families or by founding new territories.

Our observations of dominance and subordination were made on free-living jays whose family status as breeders, helpers or juveniles was known. Our interpretations suggest that in the Florida Scrub Jay intra-familial dominance is neither related to site nor associated with competition for food, but, instead, is related to the reproductive interests of the various family members.

METHODS

At the Archbold Biological Station (ABS) in Highlands County, Florida, Scrub Jays inhabit several thousand hectares of contiguous, periodically burned oak scrub (Woolfenden 1969). Beginning in 1969, jays in families occupying about 600 ha of property later acquired by ABS were color-ringed, and by 1972 virtually all individuals in about 30 families were marked. As the project continues, a gradually increasing percentage of these birds are of known age and even known parentage. The marking scheme is de-

tailed in Woolfenden (1975). With few exceptions the marked jays are extremely tame towards humans, which has enhanced greatly our opportunities to observe normal intraspecific interactions.

Observations and simple experiments intended to unravel the complex interrelationships within Scrub Jay families were made primarily after nesting had ended during June through August of 1972 and 1973. Incidental observations prior to 1972, which are not included in the tables, and the determination of the status of certain individuals after 1973 have strengthened the conclusions we present.

Detailed observations of dominance behavior were obtained for 21 families which included most of the variation in family size and constituency typical of the local population. As six families were observed during both summers, our sample includes a maximum of 27 jay-family summers. Most of the encounters we recorded were induced by offering the jays morsels of peanuts. A simple, portable, gravity feeder, which provided one morsel at a time when a bird approached from a certain direction, often was used. Dominant birds approached the feeder at will, often supplanting a subordinate, and defended their new position against other family members. By forcing close contact between the jays, we increased the frequency of interaction and thereby increased our sample of observations.

RESULTS

DOMINANCE BEHAVIOR

A variety of interactions, ranging from mild to intense, demonstrate aggression in the Florida Scrub Jay. In general, active aggression includes supplanting and threat postures that elicit submissive behavior from the recipient. Long chases, during which the subordinate utters submissive notes while dodging the closely pursuing dominant, also occur. Occasionally, mild encounters erupt into more intense conflict. During a fight, the two birds usually grasp each other's legs with both feet, and, as they roll onto their sides, the dominant bird scolds and pecks while the subordinate utters intense submissive notes. The conflicts, which immediately draw the attention and close approach of other jays, last only a few seconds. Virtually all aggressions are initiated by individuals that eventually are victorious and, thus, are the dominant birds.

Subtle indications of dominance relationships include submissive postures and vocalizations by the subordinate bird. We take a

* We dedicate this paper to Richard Archbold (1907-1976), benefactor of biology and friend.

TABLE 1. Aggressive encounters within 21 Florida Scrub Jay families during 27 jay summers.

Dominant	Subordinate					Total Victories	Percent Victories
	Male Breeder	Male Helpers	Female Breeder	Female Helpers	Juveniles Sex Unk.		
Male breeder	—	$\frac{107}{115}(20)^a$	$\frac{40}{44}(27)$	$\frac{23}{23}(10)$	$\frac{18}{18}(25)$	$\frac{188}{200}(82)$	94
Male helpers	$\frac{8}{115}(20)$	— ^b	$\frac{89}{89}(20)$	$\frac{53}{54}(6)$	$\frac{28}{28}(23)$	$\frac{178}{286}(69)$	62
Female breeder	$\frac{4}{44}(27)$	$\frac{0}{89}(20)$	—	$\frac{4}{4}(10)$	$\frac{11}{11}(25)$	$\frac{19}{148}(82)$	13
Female helpers	$\frac{0}{23}(10)$	$\frac{1}{54}(6)$	$\frac{0}{4}(10)$	— ^b	$\frac{10}{17}(15)$	$\frac{11}{98}(41)$	11
Juveniles sex unk.	$\frac{0}{18}(25)$	$\frac{0}{28}(23)$	$\frac{0}{11}(25)$	$\frac{7}{17}(15)$	— ^b	$\frac{7}{74}(88)$	09
Total defeats	$\frac{12}{200}(82)$	$\frac{108}{286}(69)$	$\frac{129}{148}(82)$	$\frac{87}{98}(41)$	$\frac{67}{74}(88)$	—	—
Percent defeats	06	38	87	89	91	—	—

^a The denominator for each fraction represents total encounters, the numerator the number of victories for the dominant and number of defeats for the subordinate. Opportunities for jays of different status to interact, based on the composition of all families of jays, are given in parentheses as jay summers.

^b Encounters between family members of the same status are discussed in the text.

conservative approach and list in table 1 only the aggressive dominance encounters; table 2 tallies the submissive gestures. Comparison of tables 1 and 2 shows that aggressive dominance encounters and submissive gestures disclose the same fundamental dominance relationships within Florida Scrub Jay families.

Both paired and unmated Florida Scrub Jays attempt to pass food to other jays. Among paired jays, passing food probably serves to strengthen the pair bond and stimulate breeding. Among unpaired jays of opposite sex and different families, it probably functions in pair formation. Attempts to pass food to jays of the same sex and in the same family cannot have these functions. Where this occurred, other interactions showed that the dominant jay fed the subordinate; often such attempts immediately followed an active supplant or chase. Thus we suspect offering food is an expression of dominance in Florida Scrub Jays. However, we take the conservative approach and do not include food offering in the dominance interactions summarized in table 1.

Even though individual Florida Scrub Jays may live together in the same territory for many years, physical contact between them is rare. Excluding passing food, copulation, and

certain activities of juveniles described later on, these jays rarely touch each other except during outright fights. Activities such as allopreening, which is a dominance display in many birds (Harrison 1965), and communal roosting have not been observed.

Outwardly, peaceful coexistence typifies the relationships among Florida Scrub Jay families. During one continuous 6 h observation period of a family of six jays foraging for natural foods, only eight dominance encounters occurred, including no fights. In contrast, 55 encounters were induced in this same family during four accumulated hours of artificial feeding (table 3). Natural intrafamilial aggression seems most intense when nestlings exist, although as yet we have no measure of frequency under this condition. With all 21 families, the encounters we induced paralleled those that were observed during natural foraging. It is our impression that dominance relationships may be firmly established within families, and rarely need to be displayed overtly.

INTRAFAMILIAL DOMINANCE

The composition of the 21 jay families chosen for study varied from simple breeding pairs to pairs with one to four helpers of either sex, rearing zero to four juveniles. Hence the

TABLE 2. Submissive gestures within 21 Florida Scrub Jay families during 27 jay summers.

Dominant	Subordinate					Total Victories	Percent Victories
	Male Breeder	Male Helpers	Female Breeder	Female Helpers	Juveniles Sex Unk.		
Male breeder	—	$\frac{46}{48}(20)^a$	$\frac{46}{46}(27)$	$\frac{11}{11}(10)$	$\frac{11}{11}(25)$	$\frac{114}{116}(82)$	98
Male helpers	$\frac{2}{48}(20)$	— ^b	$\frac{19}{19}(20)$	$\frac{3}{3}(6)$	$\frac{6}{6}(23)$	$\frac{30}{76}(69)$	39
Female breeder	$\frac{0}{46}(27)$	$\frac{0}{19}(20)$	—	$\frac{6}{6}(10)$	$\frac{14}{17}(25)$	$\frac{20}{88}(82)$	23
Female helpers	$\frac{0}{11}(10)$	$\frac{0}{3}(6)$	$\frac{0}{6}(10)$	— ^b	$\frac{3}{4}(15)$	$\frac{3}{24}(41)$	13
Juveniles sex unk.	$\frac{0}{11}(25)$	$\frac{0}{6}(23)$	$\frac{3}{17}(25)$	$\frac{1}{4}(15)$	— ^b	$\frac{4}{38}(88)$	11
Total defeats	$\frac{2}{116}(82)$	$\frac{46}{76}(69)$	$\frac{68}{88}(82)$	$\frac{21}{24}(41)$	$\frac{34}{38}(88)$	—	—
Percent defeats	02	61	77	87	89	—	—

^a as in footnote a, table 1.^b as in footnote b, table 1.

opportunity for jays of different status to interact varied. This variable, computed in jay summers, is listed in parentheses for each combination in tables 1 and 2. For example, the family whose interactions are summarized in table 3 contained three male helpers in 1973; thus it contributes three male breeder-male helper jay summers to the sample of 20 listed for that combination in tables 1 and 2. As aggression between family members is infrequent, we assume that even in families with two or more jays of the same status, each jay has an equal, independent opportunity to be involved in encounters with all other family members. All 21 families bred immediately prior to the two summer observation periods. cursory observations during other seasons convince us that dominance relationships are similar throughout the year in stable families.

Unless otherwise stated, the interactions compiled in tables 1 and 2 appeared typical of all families during the 27 jay summers. To preserve this regularity we delete from table 1 44 defeats sustained by one female helper from an aberrant family. This and one other unusual family are discussed separately.

As monogamy is the rule in Florida Scrub Jays, no opportunities for intrafamilial conflicts between breeding males or breeding females existed in 1972 and 1973. However, in

1974 a unique case of bigamy occurred in which one female clearly and consistently dominated the other (Woolfenden 1976). Helpers of the same sex coexist in some families as do sibling juveniles. Interactions between individuals of the same family status are excluded from tables 1 and 2 and are treated in the text.

As victories in aggressive encounters nearly equal number of encounters initiated, their frequency serves as a relative measure of aggressiveness. Males won 366 encounters in 151 jay summers, females only 30 in 123. Furthermore only 7 of 37 females were seen to initiate any encounters. From these data we conclude not only that male Florida Scrub Jays are more aggressive than females, but also that most females lack intrafamilial aggressive tendencies altogether.

Males won 205 (98%) of 210 aggressive encounters with females. Clearly male Scrub Jays dominate females; this is true even when the male is a helper. Male helpers dominated breeding females, who usually were their mothers, in all 89 encounters, and they dominated female helpers in 53 of 54 encounters. Male helpers dominated the female breeder in 15 of the 20 jay summers, and in 3 of the remaining 5, either the helper or the female was shy and difficult for us to observe at close range.

TABLE 3. Dominance relations in one family of Florida Scrub Jays during the summer of 1973.

Dominant	Subordinate						Total Victories
	R-PS♂	YdGS-♂	PiS-R♂	IBS-R♂	dGR-S♀	dGdGS-♀	
R-PS ♂ Breeder	-	1,3 ^a	4,4	1,2	1	1,1	7,11
YdGS- ♂ Helper		-	8,6	11		4	23,6
PiS-R ♂ Helper			-	22,5	1,3	6	29,8
IBS-R ♂ Helper				-		3	3
dGR-S ♀ Breeder					-		0
dGdGS- ♀ Helper			1			-	1
Total Defeats	0	1,3	13,10	34,7	1,4	14,1	63,25

^a First number denotes victories by the dominant jay, the second denotes submissive gestures by the subordinate.

Many times, in numerous families, we saw the male breeder intervene and terminate aggression directed at his mate by a male helper. While this appears not to reduce the frequency of encounters, it often reduces their duration and severity. Often these interventions culminated in a short chase of the helper by the male breeder. To date we have not seen this behavior between any two birds other than male breeder and male helper. This may indicate the intensity with which male breeders enforce their dominance over male helpers, an idea we return to later.

As shown in table 1, breeding females were dominated by their mates less often than by their male helpers (40 aggressions in 27 jay summers versus 89 in 20, respectively). However, the breeding male received more submissive gestures from the breeding female than did helper males, as shown in table 2 (46 in 27 jay summers versus 19 in 20). We suspect these differences reflect the close relationship, often of many years' standing, between these nearly permanently monogamous breeders as compared with the generally shorter-term relations between females and their sons.

As male dominance is the rule, the only potential challenge to a male breeder comes from his male helpers, and male breeders clearly dominate. Of 115 aggressive encounters between them, 107 (93%) were won by the breeder. All 8 reversals were by a single male (IGWS-), a bold and aggressive individual whose father seems more docile than most breeding males. The 115 encounters occurred in 18 of the 20 jay summers; in the

remaining two, submissive behavior by the helper confirmed his subordination to the male breeder.

Aggression by male breeders actually appears to be preferentially directed toward their male helpers. Of 170 victories by male breeders over nonjuvenile family members, 107 (63%) were against male helpers. However, male helpers outnumber female helpers (Woolfenden 1975), which is reflected in their respective samples in table 1. To reduce this bias we divided total victories by total jay summers in the breeding male over helper male sample, and in the breeding male over breeding and helper female samples taken together. Thus 107 victories divided by 20 jay summers is compared with 63 victories (40 + 23) divided by 37 jay summers (27 + 10). The results, 5.4 victories by breeding males over helper males versus 1.7 over females, strengthen the conclusion that breeding males are especially aggressive toward male helpers. Even when victories by male breeders over male helpers are compared only with those over female helpers (23 aggressions in 10 jay summers), the difference remains clear (5.4 versus 2.3).

Only 4 aggressions and 6 submissive gestures were noted between a female breeder and a female helper. All were won by the breeder. The rarity of female-female encounters supports the contention that female Florida Scrub Jays nearly lack intrafamilial aggressive tendencies.

It is evident that Florida Scrub Jay families contain a dominance structure in which male breeders dominate all other family members,

male helpers dominate females, and female breeders are mildly dominant over female helpers. This ranking into a dominance hierarchy correlated directly with success of the respective family members in aggressive encounters and with receipt of submissive gestures (tables 1, 2, right-hand columns).

The vagaries of reproduction and mortality result in relatively few families having male helpers of different ages. During the summers of 1972 and 1973, three such families were studied, one of which retained two of its three male helpers through the 1974 breeding season. From 1971 through 1975 six additional families, in which repeated aggressive encounters were noted by Woolfenden, contained male helpers of different ages. In eight of these nine instances the older males clearly dominated their younger sibs. The only exception (IGWS- δ dominating dGYS δ) is discussed below. Since 1971, four sets of male brood mates have been studied, and even in the absence of age differences, one male helper consistently dominated the other. Thus it seems that whenever male helpers coexist in a family, a dominance hierarchy is established between them. Table 3 presents an example of one such family in which aggressive relationships between male helpers were especially clear. It also shows the subordinate positions of female family members.

The duration of females as helpers tends to be shorter than that of males (Woolfenden 1975); thus our sample of families with two or more helper females is even smaller than that for males. Furthermore, as already shown, aggression by females normally is rare. One family studied in 1972 included two female helpers differing in age by one year. During six accumulated hours with this family, special effort was made to induce interactions between the females, but none was observed. However, in another family four juvenile females established a clear dominance hierarchy during the summer of 1973 prior to their first opportunity to help (table 4). Thus hierarchies may exist among female helpers, but they are difficult to discern and remain unsubstantiated.

Young jays begin foraging about one month after fledging. At this time experimentation with their surroundings gradually increases the frequency of interactions with siblings. Young juveniles often initiate exchanges of mild nips by pecking at the wings or tail of siblings. Often the exchanges erupt into fights or long chases with one individual

TABLE 4. Dominance relations among four brood mate juvenile female Florida Scrub Jays.

Dominant	Subordinate				Total Victories
	S-dBW ♀	S-YW ♀	S-IGW ♀	S-PW ♀	
S-dBW ♀	—	2	6	9,1 ^a	17,1
S-YW ♀	1	—	7	4	12
S-IGW ♀			—	3,1	3,1
S-PW ♀				—	0
Total Defects	1	2	13	16,2	32,2

^a First number denotes victories by the dominant jay, the second denotes submissive gestures by the subordinate.

usually dominating. As the young birds mature, these investigative encounters grow more stereotyped and their outcome more predictable, as typifies those of older birds.

We observed 142 interactions clearly enough to consider them dominance encounters between juveniles. Table 4 lists those between four brood mates and provides our best example of a juvenile dominance hierarchy. In the only other family containing four juveniles, the hierarchy was less defined though we did record twice as many aggressions (17) by the dominant juvenile as by any other and witnessed none by the bottom-ranking individual. In all other families studied, linear hierarchies invariably were established among all juvenile members. The apparent absence of interactions between nestlings and between recently fledged young leads us to suspect that juvenile dominance relationships originate as young jays begin to forage and gain independence about one to two months after fledging.

Members of a Florida Scrub Jay family occasionally clash when seeking a food item. However, once an individual has taken the morsel, other jays normally direct their attention elsewhere. If the item taken is large, such as a tree frog, lizard, or large insect, the possessor quickly moves off a short distance in order to tear it up for swallowing. Semi-independent juveniles might be expected to suffer in this competition because of their ineptitude, but we have noticed two seemingly compensatory practices. Older jays often will turn away from a morsel of food after discovering it, thereby giving a juvenile an opportunity to take it. Not only does this behavior of older jays allow juveniles access to food, but also it may teach them foraging techniques. More remarkable is a form of supplanting, apparently practiced only by juveniles, in which the young birds gently land on the back of another individual, including adult-plumaged jays. Though infrequent, we

have witnessed this act several times, especially with birds that come to the hand for peanuts; the bird whose back is touched always retreats. Lorenz (1970) described similar behavior in Jackdaws (*Corvus monedula*) and other unnamed passerines, and suggested that it may be a means by which adults show juveniles suitable perches. While this may be true, we suspect that it also may function to provide food for the less coordinated juveniles. This behavior disappears following post-juvinal molt. With these rare instances excluded, we never saw a juvenal-plumaged jay dominate an adult-plumaged jay. During early summer, juveniles require feeding by older family members, but even after this period of physiological dependency, they continue to beg in a submissive manner. The seven aggressive encounters won by juveniles over adults (table 1) and the four submissive gestures toward juveniles (table 2) occurred during post-juvinal molt. As these 11 victories were over females, we suspect that the victors were maturing males. Unfortunately all five juveniles involved disappeared before their sex could be determined by other means.

Occasionally, abnormally aggressive relationships exist between replacement breeders and the resident non-breeders. As these situations may shed some light on the functions of intrafamilial dominance, we report on two such aberrant families, one involving a replacement female and one a replacement male.

In March 1973, a female (-IGRS) replaced an injured breeder. A helper female hatched in this territory in 1972 tended to remain with her injured mother, apart from the newly forming pair. Following the presumed death of the injured bird, the helper rejoined her father. His new mate was at once conspicuously aggressive toward her stepdaughter with whom she was unfamiliar and whom she presumably considered to be a potential rival. As mentioned earlier, we deleted from table 1 the 44 victories over her unrelated helper by this female. She also accounts for the four wins by a female breeder over her mate (table 1), all of which immediately followed intense aggressions by the female toward her stepdaughter.

Another example of strong aggression by a replacement breeder (-ORS♂) toward the offspring of his new mate was detailed by Woolfenden (1975: table 8). In this case, continued severe aggression by the replacement male immediately preceded the departure of two male helpers from the territory.

As they did not disperse to breed, we suspect that their departure was a result of the strong dominance by the new breeder. The two younger birds succeeded in joining another pair, for whom they became helpers.

Dispersing Florida Scrub Jays regularly return to their natal territory with no change in status within the family hierarchy. Dispersal forays, more conspicuous among females, often persist for many months, with the disperser returning to his or her home territory daily. Even following departures of longer duration, jays occasionally visit or rejoin their families. In one example, a female (-IBYS) who hatched in 1970 and helped in 1971 bred nearby in 1972 and 1973. Following divorce, which is rare, she returned to her natal territory where she was tolerated by her parents. A helper male, who had no previous contact with this female, his sister, seemed unusually aggressive toward her, but she remained in the territory as a subordinate. A similar case involved the return by a male (-WWS) to his natal territory following the death of his mate. The returning male was strongly dominated by his father, but dominated his stepmother in his father's absence. In general, the probability of a jay rejoining its family appears greatest when the returning bird's parent of the same sex remains alive. While aggression became more pronounced, no change in status within the family hierarchy resulting from these returns was witnessed.

Florida Scrub Jays appear to have a strong drive to be members of a group. We have never known a lone bird to reside in one place very long, and on several occasions we have watched lone jays attempt to join established families. Sometimes, through persistence, they succeed. Following the disappearance of breeders, any remaining non-breeders in a territory often stay together for several months, sometimes throughout a breeding season. We studied one such group, in which both breeders had recently disappeared. The four remaining sibs, including two males and at least one female, retained a normal hierarchy throughout one summer and successfully defended their territory from intruders. Later one bird disappeared, and the other three dispersed and bred.

DISPERSAL OF MALE HELPERS

Our conclusions regarding certain functions of intrafamilial dominance are based on the order in which coexisting male siblings disperse for breeding. In 14 cases since 1970

TABLE 5. Time of pairing of 22 male Florida Scrub Jays from 10 families that contained two or more male helpers.^a

Male Helpers	Year		
	Hatched	Helped	Paired
WW-S>>	1969	1970	1971 (Feb)
YY-S>	1969	1970-72	1973 (Feb)
-dGWS	1970	1971-73	D1973 (Aug)
-dBdGS>	1970	1971	1971 (Jul)
-PdGS	1970	1971-72	†1972 (Apr)
Pi-dGS>	<1969	<1970-71	1972 (Mar)
-OdBS	1970	1971	1972 (Apr)
Pi-RS>	<1969	<1970-71	1972 (Mar)
-WWS	1970	1971	1972 (Apr)
-ORS>	1970	1971	1972 (Mar)
-PiRS	1970	1971-72	1973 (Mar)
R-PiS>	<1969	<1971-72	1973 (Jan)
ORS-	1971	1972	†1973 (Jun)
-IGIGS>	1970	1971-73 ^b	1973 (May)
P-SdG	<1970	<1971-72	1973 (Jan)
dBR-S>	1969	1970-73	1973 (May)
-WdBS	1970	1971-73	1974 (Feb)
dG-YS	<1968	<1971-74 ^b	1975 (Mar)
IGWS->?	1971	1972-74	1975 (Mar)
YdGS->>	1971	1972-75 ^b	—
PiS-R>	1972	1973-74	1975 (Mar)
IBS-R	1972	1973	1974 (?)

^a Spaces separate helpers of different families, > identifies jays known to dominate their siblings, >? indicates dominance is uncertain, D indicates disappeared, and † indicates died.

< before a year identifies individuals of unknown age, who may have hatched and helped in years earlier than those indicated.

^b Exceptions to the generalization that dominant male helpers breed first are discussed in text.

we have witnessed the pairing of a male helper from a family that included two, or in one case three, male helpers. In 9 of the 14 cases the dominant male definitely was the first to pair (table 5). Furthermore, four of the five seeming exceptions are equivocal. In one, the subordinate (P-SdG ♂) was not a sibling (see Woolfenden 1975: table 9). Both he and -IGIGS ♂ courted a neighboring widow, and, although -IGIGS ♂ appeared to dominate the unrelated helper, P-SdG ♂ succeeded in obtaining the female as his mate. -IGIGS ♂ remained and helped for four months, then he departed and bred. A second case involved the simultaneous pairing by two brothers (dG-YS ♂ and IGWS-♂) with a widowed female and her daughter, respectively. Previously, this had been our only instance of a younger male dominating his older brother, but our dominance observations were confounded in that IGWS-♂ was extremely bold while his brother was shy and retreating in our presence. It is noteworthy that the older male paired with the older and more experienced female, with whom the probability of successful breeding is greater (Woolfenden 1973).

The three remaining exceptions pertain to the family whose dominance relationships are depicted in table 3. YdGS-♂, who for the first part of the 1975 breeding season remained with his parents as a helper, attempted to pair in December 1974, three months before his subordinate sib PiS-R ♂ dispersed and paired. However, in February 1975, YdGS-♂ returned to his natal territory, having failed to pair with the female who became the mate of dG-YS ♂ (see above). His failure to pair may have been related to an infected injury on his cheek, forehead and mandible, first noted in February. IBS-R ♂ dispersed before both his dominant sibs, and we treat this as two exceptions. However, even though he seemingly was paired in 1974, we found no evidence of breeding until March 1975, which was essentially simultaneous with that of his brother PiS-R ♂. Thus the breeding of IBS-R ♂ prior to the pairing of his older sib, YdGS-♂, is our outstanding exception to the general rule that older and dominant male helpers pair first. We are tempted to suspect that the frequency of aggression toward IBS-R ♂ by his dominating sibs (table 3) may have caused his early departure.

INTERFAMILIAL DOMINANCE

The close relation between dominance behavior and territoriality has been noted by many authors. By measuring dominance at feeding stations established near the nests of several Steller Jays, Brown (1963) found a direct correlation between the ranks of individuals in a flock and the flock's proximity to their respective nests. Brown emphasized the continuum between different dominance systems that was first postulated by Davis (1958, 1959). At one end are flocking species with invariant hierarchies; intermediate are species whose peck order varies topographically, each individual gaining top rank near its nest. At the opposite end are species in which each pair totally dominates in the area surrounding its nest, which becomes an exclusive territory.

Scrub Jays exemplify the latter extreme in Davis' continuum, especially in western North America where only pairs defend territories (Verbeek 1973). In Florida, pairs regularly retain yearlings and older jays as helpers in their permanent territories. Thus many territories are occupied continuously for several years by family groups, within which we have shown a dominance structure unrelated to territoriality.

In Florida Scrub Jays, territorial defense

usually is initiated by a single member of a family who almost always is soon joined by all other adult-plumaged jays. We measured each family member's contribution to defense of the common territory by noting which bird was the first to respond to natural trespasses by neighboring jays ($n = 48$) and to playback experiments with recorded territorial scolding ($n = 122$).

We divided the total number of responses of family members of different status by their number of opportunities to respond. The percentages total more than 100 because in a few cases two birds initiated simultaneous responses. The results are

Male Breeder: 86 responses in 170 opportunities = 51%;

Female Breeder: 59 in 170 = 35%;

Male Helpers: 18 in 93 = 19%;

Female Helpers: 1 in 46 = 2%;

Juveniles: 6 in 90 = 7%.

These data show that the breeding pair initiates most territorial defensive actions (86%) and that breeding females are significantly faster in responding than are helper males. Thus breeding females seem more aggressive than helper males during interfamilial encounters, while the reverse is true within the families. During territory defense, females vocalize and display vigorously, and while incubating or brooding, they leave the nest readily to do so. However, they engage in fewer outright chases and fights than do their mates. The absence of a parallel between an individual's rank in the family hierarchy and its contribution to territorial defense exemplifies the independence of intrafamilial and territorial dominance in the Florida Scrub Jay.

Juvenile jays frequently wander short distances from their home territories during their first summer. Occasionally several juveniles from different families wander together in temporary bands of varying composition. This behavior may be a vestige of the fall flocking habits still characterizing western North American Scrub Jays whose social structure appears to be more primitive than that of the Florida race (Brown 1974). Adult-plumaged jays rarely chase these wandering juveniles as long as the trespassers retain their brown-headed immature plumage (Pitelka 1951). The frequent begging by these wanderers is ignored by jays from other families. As post-juvinal molt nears completion, territorial aggressions toward these young (but now essentially adult-plumaged birds) increases markedly. By the end of their first

autumn the juveniles, repeatedly attacked by all jays outside their own families, normally return to their natal territories and begin contributing to territory defense.

NEUTRAL GROUNDS

Cracked corn is distributed daily on the Main Grounds near the buildings at ABS providing an artificial situation that resembles Brown's (1963) experimental feeding stations. During certain seasons, Scrub Jays from many families make brief visits to the Main Grounds to obtain this food. Thus for several short periods each day numerous jays from many (but not all) territories forage together in a neutral area. Relations among them contrast strongly with those reported for the Steller Jay, in which aggressions sometimes were too frequent for Brown (1963) to record. Especially in view of their vigorous territorial aggression, fighting between Scrub Jays on the Main Grounds is conspicuously rare. In the summer of 1972 during 20 hours of observation with 7 to 20 jays present, we saw only 42 aggressions. Nineteen of the 42 were initiated by breeding adults; of these, 13 were executed by the pair whose territory borders the Main Grounds. Breeding birds from several families often feed within inches of one another, or even with tails overlapping, without aggression.

It seems unlikely that Scrub Jays in Florida ever congregate in such neutral areas under entirely natural conditions, although flocks of non-breeders are reported for a population from western North America (Westcott 1969). To the contrary, we suspect that dispersal forays by helpers account for most normal movements of adult jays across territorial boundaries. The striking contrast between aggressive tendencies of Florida Scrub Jays on their territories and on the Main Grounds at ABS points to the limitations inherent in studying a species' social organization only under artificial conditions.

DISCUSSION

Dominance hierarchies in gregarious birds classically have been interpreted as resulting from intraspecific competition for limited food. Through a peck order, dominant individuals are insured sufficient food to survive and reproduce, while those lower in the order survive only when resources are abundant (e.g., Lockie 1956, Fretwell 1969). Intuitively it seems unlikely that the function of hierarchies in the long-lived, monogamous Florida Scrub Jay would be to parcel their widely dispersed food preferentially to the

dominant males. Nevertheless, we can test the possibility by examining the sex ratio of yearling jays. Virtually all individuals remain in their natal territory beyond one year, and we were able to verify the sexes of surviving one-year-old jays from five year classes (1969–1973). Assuming an equal sex ratio at hatching, a pre-dispersal sex ratio skewed toward males would be consistent with the food parcelling hypothesis. Instead, exactly 50% of the 68 yearling survivors were the subordinate females. Even when examined separately, none of the five year classes shows a strong preponderance of either sex. This is the result despite the fact that the study period includes the worst drought in 40 years and exceptionally cold and warm winters (Woolfenden 1973).

Further evidence that dominance in Florida Scrub Jays is not related to competition for food is provided by data on weights of fledgling, helper, and breeding jays from all months of the year. Were starvation a regular cause of Scrub Jay mortality, we would expect to find at least a few jays with greatly reduced body weights. Few such birds have been found, and two grossly underweight juveniles that were discovered near death proved to be badly infested with nematode parasites (Kinsella 1974). Moreover, most jays in the study tract react toward humans as a food source, and starving birds would thereby make their plight obvious to us. We encounter such individuals extremely rarely. Finally, we found no correlation between dominance and survival for the 25 fledglings studied in 1972 and 1973, which contrasts with the speculation of A. Zahavi (pers. comm.).

In our view, five independent relationships account for dominance ranking within Florida Scrub Jay families. They are 1) strong dominance by a breeding male over his male offspring; 2) competition between male helpers; 3) dominance by a helper male over his mother; 4) general weakness or absence of female aggressiveness toward all family members; and 5) frequent interactions among juveniles. These components of the family hierarchy, all of which appear ultimately to be associated with optimizing each individual's reproductive potential, are analyzed separately in our interpretation of intrafamilial dominance in this species.

MALE BREEDER—MALE HELPER

The presence of more than one male in a territory produces the potential for com-

petition between them for the opportunity to mate with the resident female breeder. Therefore, if he is to permit additional males in his territory, a breeding male should reduce as much as possible their potential threat to his reproductive investment. The strong dominance by the male breeder over his sons probably protects the breeder's reproductive position in two ways. First, it ensures that he alone contributes genes to the future offspring of his mate. Second, it prevents a helper from taking over the territory, or too large a part thereof (see below), as his own. Several details relating to the dominance of breeding males are consistent with the first suggestion. Males are especially intolerant of any helper near the nest bush. Whether this be to prevent cuckoldry or to protect the nest contents, or both, remains unknown, but aggressiveness by male breeders is most intense during the earliest stages of the nesting cycle, the period in which copulation occurs and parentage is determined. Intense aggressiveness by the male breeder during the egg stage of nesting was especially conspicuous during two attempts at a second brood, both by the same pair with the same male helper. The male breeder initially was as aggressive as usual during the first nesting, and his aggression waned throughout the nest period. The helper was permitted to feed nestlings and fledglings without conflict, and even to feed the incubating female toward the end of incubation. Upon commencement of the second nest, however, the breeder's aggressiveness returned suddenly and dramatically. The helper was repeatedly attacked and chased over much of the territory, and was not tolerated within about 5 m of the new nest. Often during this period, when the breeding male approached this helper anywhere in the territory, the latter begged submissively. Again the breeder's aggressiveness diminished as incubation progressed, and the helper was permitted to feed the second brood as actively as he fed the first.

Dominance over his male helpers also may provide an advantage to a male breeder who must form a new pair following the death of his mate. Three times we have seen recently-widowed males pair with females whom their sons had been courting for months, and in no instance has a male breeder tried to do so and failed. Through their dominance, experienced breeders may outcompete their sons when both are courting.

We know of no instances of pairing between

closely related Florida Scrub Jays, which suggests that the relationship between son and mother may normally preclude copulation. If this is the case, the strongest aggression by a male breeder toward his son should exist when the son's mother is replaced by an unrelated female who has no established relationship with her new stepson. In three such families aggression by the breeder did become noticeably more intense following the replacement of his mate, though this was not quantified.

We interpret the extreme aggression by stepfathers toward their stepsons as further evidence of the importance to a male breeder of insuring his reproductive investment by dominating all other males in the territory. Stepsons probably are tolerated, in general, because of their potential contributions to territorial and nest defense, and the feeding of young (Woolfenden 1975). Being unrelated, however, a stepfather has no further selective interest in their well-being. Without the buffer of parenthood, therefore, his aggressive behavior toward a stepson, who remains an unrelated potential rival within the territory, is predictably more intense.

MALE HELPER—MALE HELPER

Even though helping may last for several years, it is transitory, for ultimately all jays must breed if they are to contribute genes to the population more directly than helping permits. Hence intrafamilial competition for the opportunity to breed exists whenever two or more helpers of like sex coexist in a family. We interpret dominance between male helpers as a manifestation of this competition. As we have stressed in our analysis of table 5, usually the higher ranking male is the first to pair, and therefore probably to breed. Most often first breeding occurs after dispersal of older male helpers whose continued dominance over siblings they helped raise insures them precedence when breeding space becomes available. Even when two similarly-aged males coexist, dominance invariably is established by one, who thereby insures his precedence should a vacancy arise. The importance of dominance behavior in determining future reproductive advantages in this population parallels the observation by Smith (1976) that alpha male Black-capped Chickadees (*Parus atricapillus*) among winter flocks obtain the better quality breeding territories in the spring. However, it remains unsubstantiated whether tit dominance relationships deter-

mine, or are determined by, local territorial holdings of the flock members.

Dispersal is not the only way a male can become a breeder. A second option is to take over part of his natal territory and, with help from a new mate, defend it as his own. We wish to emphasize the possibility that delaying breeding in order to inherit a portion of the natal territory in some instances may have advantages that outweigh those of early dispersal. Dispersal always includes moving to unfamiliar ground and defending entirely new territorial boundaries. For this reason it seems more accurate to hypothesize that by dominating his sibs a male helper ensures his option either to remain or to disperse when the opportunity arises. Thus selection may favor retaining males in the population who tend to remain in their natal territory for more than one year.

MALE HELPER—FEMALE BREEDER

The simplest interpretation of the dominance of male helpers over their mothers is that it reflects selection for male aggressiveness and female passiveness. However, it also could result from an independent evolutionary strategy, as it would seem to be in his best interests for a male helper to increase his chances of becoming a breeder in his natal territory in the event of his father's death. Dominating his mother might facilitate expelling her from the territory, permitting his pairing with an unrelated female were his father to die. However, in the only case to date by which we could test this hypothesis, the breeding female repaired normally, and her son remained as a subordinate and helped his stepfather for two subsequent breeding seasons. It may be that the rapid arrival of a replacement breeder often precludes the helper male from becoming a breeder in these instances. In any event, additional observations presumably will provide further test cases. We predict that they will provide further evidence against the possibility that males routinely expel their widowed mothers from their home territory.

FEMALE—FEMALE

Intrafamily dominance by female Scrub Jays, either breeders or helpers, is rare and appears to reflect their general lack of aggressiveness. Our observations on dispersal and pairing by females suggest that their passive behavior itself may be adaptive. A female breeder is aggressive toward dispersing fe-

males and drives them away. An unpaired male also is aggressive, but his aggression diminishes as an intruding female persists by evading his threats. Gradually his aggression wanes and shifts to courtship, which then requires submissive postures and vocalizations by the female. Intrafamily passiveness persists throughout the life of a paired female, even though her interfamily aggression increases once the pair bond is firm. Thus, we suspect that individual females whose passive temperaments facilitate dispersal and rapid pair formation are selectively favored. Therefore submissive behavior in intrafamily interactions would seem to have long term adaptive value for female Florida Scrub Jays. Evidence consistent with this hypothesis is provided by Castoro and Guhl (1958), who found that submissive behavior by females increased the efficiency of pair bond formation in caged pigeons (*Columba livia*). The least aggressive females paired first.

The possibility exists that dominance over female helpers by other family members (table 1) prompts their repeated dispersal forays and early departure from the territory. However, we have no evidence that food supply limits family size in the relatively large territories of Florida Scrub Jays. Furthermore, as we have shown, intrafamilial aggression is infrequent and not severe. Thus the hypothesis that helper females are driven from their natal territory through dominance remains moot.

JUVENILES

The aggressive encounters and investigative pecks of juvenile jays, both of which decrease as the birds mature, often include postures and vocalizations characteristic of adult display. These interactions probably facilitate development and expression of roles important to their later positions in the family and the population. Thus juvenile dominance behavior can be viewed with the same adaptive interpretations associated with play behavior in mammals (Bekoff 1972).

CONCLUSIONS

The cooperative breeding systems of many birds, including certain garruline corvids, appear far more complex than that of the Florida Scrub Jay, especially because the reproductive groups include more than one breeding pair (Brown 1970). Reports of numerous behavioral modifications for certain of these group breeders suggest to us that

their social development has had a relatively long evolutionary history.

In contrast, the social system of the Florida Scrub Jay is relatively simple and appears to exhibit a preliminary stage in the evolution of communal breeding. Many corvids, including Scrub Jays in western North America, breed as lone pairs in exclusive territories (Verbeek 1973, Brown 1974). Possibly related to their confinement in a relict, patchy habitat, Scrub Jays in Florida profit from delaying breeding for one to several years and remaining in their parental territory during that time. Thus the major, and probably evolutionarily recent development in the Florida Scrub Jay social system is the long-term existence of potential breeders within a pair's territory. Among the first behavioral modifications to arise in response to this situation seem to be the simple dominance-subordination relationships we have described for family members. Through these relationships, individuals continue to establish their actual or potential reproductive positions in the population while retaining the advantages of living in a family group.

SUMMARY

We studied dominance behavior in a color-ringed population of Florida Scrub Jays during six years of general observations and two summers of intensive study of intrafamilial and interfamilial aggression. Encounters were recorded from 21 families of varying size and constituency. The jays are extremely tame, which facilitated watching their normal behavior; we augmented these observations with simple experiments involving the offering of tidbits of food.

The Florida Scrub Jay, a permanently territorial group breeder, exhibits a social dominance structure in which the male breeder dominates all other jays in the family, male helpers dominate all females, and the female breeder mildly dominates female helpers. Juveniles, subordinate to all other family members, seem to establish a hierarchy among themselves through investigative encounters during their first summer.

Whenever two or more male helpers coexist in a family, a hierarchy exists between them. Usually the dominant male helper is the first to depart and pair when a breeding opportunity develops. Dominant male helpers occasionally establish a new territory by gradually usurping a portion of their parents' territory.

Although dominance within the jay families is clear, aggressive conflicts are rare. This contrasts sharply with the frequency of boundary disputes between neighboring families. Involvement in interfamilial aggression, measured by summoning jays to playbacks of territorial scolding, is not directly correlated with rank in the family hierarchy, in that breeding females respond more quickly than their male helpers. During brief visits to a neutral feeding area, jays from different families often forage within inches of each other with almost no conflict.

We view intrafamilial dominance-subordination relationships as an early behavioral modification associated with the evolution of the helper system in the Florida Scrub Jay. Through dominance, family members establish their actual, or potential, reproductive positions in the population while deriving the benefits of living in a family group. Breeding males reduce the threat of cuckoldry or loss of territory by dominating their male helpers. The probable timing of breeding opportunities for coexisting male helpers is ordered according to the dominance hierarchy established among them. Passiveness may be selectively favored in females, whose successful dispersal and pairing requires continued submissive behavior in all but territorial displays. Finally, juvenile dominance behavior may facilitate social development through use of postures and vocalizations important to their future activities as breeding adults.

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