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GROWTH AND SURVIVAL OF YOUNG FLORIDA SCRUB JAYS

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Few studies of growth in passerines pertain to jays (Corvidae: Garrulinae), and fewer still to group breeders. As a possible contribution to both topics, I measured growth rates of young Florida Scrub Jays (*Aphelocoma c. coerulescens*) raised by breeding groups of varying sizes. A notable exception to the paucity of information on corvid growth is the recent work on Piñon Jays (*Gymnorhinus cyanocephalus*), a highly social, colonial breeder that nests early in a north temperate climate (Bateman and Balda 1973). Certain comparisons are made with this species.

Florida Scrub Jays almost invariably remain in their natal territory for more than a year; therefore it was possible to obtain numerous post-fledging measurements and to monitor survival of known-age jays. The growth measure used in the analyses of survival is weight.

Florida Scrub Jays breed either as unassisted monogamous pairs or in groups consisting of a pair and several helpers. Brood size varies from 1 to 5; usually it is 3 or 4, and the number of feeders has varied from 2 to 8. Pairs with helpers fledge more young than do the unassisted pairs (Woolfenden 1975).

Preceding the weight data are brief descriptions of general development and the linear growth of certain extremities (see also frontispiece). This information should be useful for aging nestlings whose hatching dates are unknown.

MATERIALS AND METHODS

The data on growth and survival were obtained at the Archbold Biological Station in Highlands County, Florida, where a marked population of Florida Scrub Jays has been under observation since 1969. Individual jays were measured daily or, in a few cases, every other day throughout the nestling stage in 1973 when 47 nests were found, which represented virtually all nesting attempts by 28 pairs, 25 of which produced young. The approximately 136 eggs laid yielded 73 nestlings and 41 fledglings (1.5 per pair), almost

Growth stages of Florida Scrub Jays. Top left: a pipped egg and two young, age day 0. Top right: three young, age day 5, in cooling stance with necks stretched over nest rim. Bottom left: usual banding age, day 11, when primaries are breaking from their sheaths. Bottom right: a recent fledgling, age day 18.

all of which were measured in the course of this study. The productivity data show that 1973 was a near-average breeding year (Woolfenden 1973). Some measurements of nestlings and fledglings also were taken in 1974 and 1975; however, except where otherwise stated, my various analyses of growth incorporate only the 1973 measurements.

Most of the marked birds lived in open habitat, namely sparse oak scrub (Woolfenden 1969 census no. 52, 1973), and some parent and helper jays scolded loudly at human intruders. Thus nest visits by investigators were brief, lasting only a few minutes, in an attempt not to alter normal nest predation. When measuring, we removed all young from the nest simultaneously and moved several meters away; this reduced the intensity of scolding by the older jays. In addition, most nest visits were made in early afternoon (12:30–15:30) when diurnal predators seemed less active, and so that several hours of sunlight remained for the odors we left to dissipate before nocturnal predators became active. These procedures precluded obtaining detailed notes on morphological and behavioral ontogeny.

Day 0 designates the day of hatching. Fledgling and yearling are defined as before (Woolfenden 1973): fledgling is applied to a jay from the instant it leaves the nest until it is 1 year old. A yearling is a jay in its second year of existence.

The ratio between the number of jays supplying food and the number of nestlings being fed is termed the feeder index. It has ranged from 0.4 to 3.0. Nestlings with a 0.4 feeder index were members of a brood of 5 fed by a pair with no helpers; the 3.0 feeder index represents a lone nestling fed by a pair with 1 helper.

Five measurements were taken to the nearest 0.5 mm on each young jay: length of beak, tarsus, primary 7, and longest central rectrix (hereinafter referred to as a deck), and weight. The beak was measured from the anterior end of the nostril to the tip, the tarsus in a standard fashion as the diagonal from the joint with the tibiotarsus behind to the joint with the middle toe in front. The primary and the longest deck were measured from the place of attachment with the skin to the tip of the papilla or feather. Falconers use the term deck for a central rectrix and it is used here not only for brevity but also to emphasize a function of the central rectrices of shielding the lateral rectrices from abrasive wear. In Florida Scrub Jays the decks often become extremely ragged prior to replacement. Weights were taken with Pesola spring balances which were checked regularly for accuracy.

The expressions significant and highly significant are used only in the statistical sense to signify probability at the 5% and 1% levels, respectively.

Asynchronous hatching confounds the problem of measuring growth during brief once-a-day visits to nests, and in the Florida Scrub Jay hatching of eggs from the same clutch sometimes spans more than 1 day. In 1973 eggs from 9 of 25 nests probably had a time span for hatching of between 1 and 2 days. For 4 of these 9 nests, a time span between 1 and 2 days was known, and for 1 additional nest a span of 2–4 days occurred between the hatching of the first egg and last egg. The nestlings were not marked until over 1 week old, and I assumed the smaller young in such nests were the younger. In certain instances individual peculiarities allowed identification of these individuals.

Variation in time of fledging is another problem that vexes those who study growth of young birds. If undisturbed, young Florida Scrub Jays remain in the nest several days past earliest possible fledging age. In 1973, when nestlings were handled daily or every other day, almost all fledged when 15 or 16 days old, and only 1 healthy nestling remained through day 17. In 1975, when young jays were handled only on day 11, and thereafter nests were checked from convenient distances, most young fledged when 17 or 18 days old, and a few remained through days 19 to 21. Enticing their young from the nest does not seem to be an important part of Florida Scrub Jay behavior, and perhaps many nests are vacated between days 14 and 19 because of exogenous disturbances. Earliest fledging has occurred between days 12 and 14 (1 brood), the latest on day 20 or 21 (2 broods). These generalizations are based on observations at approximately 120 successful nests.

GENERAL DEVELOPMENT

At hatching Scrub Jays are naked, as typifies jaybirds, and the skin is reddish-pink, nearly identical in color to the skin of a person's hand when flushed with blood. The viscera, especially the liver, show clearly through the thin and weakly pigmented skin. The beak and legs are pale yellow. Through day 1 they get darker pink, then during days 3–4 yellowish pink. On day 2 they match the color of one's palm when it is drained of blood, and on day 3 they have the color of jaundiced human skin. During day 3 the skin becomes purple-black, usually on the back first, and the young match in color heavily bruised human skin. Darkening progresses through days 4–6 until the young are dark gray-black over most of the body, and especially dorsally. The beak becomes shiny black, the podothecae dull black.

Parting of the eyelids in nestling Scrub Jays is gradual and variable. For a few individuals the process begins as early as day 2, for some the eyes are still closed on day 9. For the majority the eyes open during days 4 through 7. Often in the same individual one eye begins opening before the other.

GROWTH

Tables 1 and 2 and Fig. 1 summarize data on growth of nestlings; they are based only on young hatched in 1973. Table 3 presents information on fledglings, for which birds hatched both in 1973 and 1974 were used. In order to provide a smooth transition in the growth data from nestlings to fledglings, the 0.5-month-old young in Table 3 are the same 20 15-day-old young in Tables 1 and 2.

Feathers.—Papillae of several tracts on the dorsum protrude prominently from the skin about day 4. Primary 7 is at least 1 mm long by day 7; the longest deck is at least 2 mm long by day 13 (Table 1). Feathers of the femoral and posterior dorsal tracts and secondary coverts of the alar tract usually break from their sheaths about day 9, with the earliest on record day 7. Primary 7 erupts between days 10 and 13, usually on day 11, and the decks erupt between days 11 and 15, usually on day 14. This rate and pattern of feathering means that young Florida Scrub Jays are only sparsely feathered until but a few days before they fledge.

The longer 7th primaries of adult-plumaged jays (age in months 24+) versus 6–12-month-old birds (Table 3) are new feathers, the original primaries having been replaced during the complete second prebasic molt. The juvenal

TABLE 1

PRIMARY 7 AND DECK LENGTHS (MM) OF NESTLING FLORIDA SCRUB JAYS

	Seventh primary				Longest deck			
Age in days	N	x̄	S.D.	Range	N	x̄	S.D.	Range
0	49	–	–	–	49	–	–	–
1	56	–	–	–	56	–	–	–
2	51	–	–	–	51	–	–	–
3	59	–	–	–	59	–	–	–
4	57	0.01	0.07	0–0.5	50	–	–	–
5	33	0.45	0.52	0–1.5	49	–	–	–
6	34	1.49	0.92	0–4	44	–	–	–
7	40	3.09	1.64	1–7	45	–	–	–
8	43	5.84	1.83	4–10	46	–	–	–
9	36	9.33	2.28	5.5–15	41	0.02	0.16	0–1
10	38	12.96	2.55	8–18	39	0.33	0.57	0–2
11	32	16.59	2.41	13–22	31	0.94	1.36	0–4
12	33	21.06	2.59	17–28	32	2.77	1.59	0–5
13	26	25.38	2.42	22–31	25	5.28	1.77	2.5–9
14	26	30.85	2.87	26–37	24	8.25	2.27	5–13
15	20	34.05	1.79	32–38	20	10.90	3.09	7–15
16	8	39.13	3.64	36–46	8	15.25	3.99	9–20

decks exist only a short time after attaining full length before they are replaced during an incomplete first prebasic molt. The longer decks of adult-plumaged jays versus 6–12-month-old birds are new feathers, the decks of the first basic plumage having been replaced during the complete second prebasic molt.

Beak and foot.—The beak of Florida Scrub Jays is little more than half full size at fledging (Table 2), and continues to grow for almost 2 months after hatching (Table 3). As the measurement taken includes both the integumentary rhinotheca and the premaxillary bones, the increase in length shown between ages 3–4 months and 6–12 months may merely reflect changes in the rhinotheca. Feeding independence is a slow, gradual process in Florida Scrub Jays, which is not fully attained for about 3 months after fledging. Perhaps this behavior reflects the slow growth of the feeding organ.

The tarsometatarsus grows rapidly (Table 2) and attains 94% adult length at fledging (Table 3). Within a few days post fledging Florida Scrub Jays escape predators by scurrying off beneath the brush. The rapid development of the leg probably accommodates this behavior. The measurements summarized in Table 3 suggest continued slow growth of the tarsometatarsus for many months or even a year post fledging, which, if real, probably reflects lengthening of the bone and not changes in the integument.

I did not measure wings of live nestlings; however, 4 specimens, age 10

TABLE 2

BEAK AND TARSUS LENGTHS (MM) OF NESTLING FLORIDA SCRUB JAYS

Age in days	Beak N	Beak x̄	Beak S.D.	Beak Range	Tarsus N	Tarsus x̄	Tarsus S.D.	Tarsus Range
0	49	3.00	0.10	2.5–3.5	51	8.81	0.35	8–9.5
1	55	3.20	0.32	3–4	51	9.66	0.63	8.5–11
2	52	3.59	0.33	3–4	54	10.97	0.90	9.5–13
3	58	3.93	0.36	3–4.5	56	12.73	1.06	10.5–16
4	51	4.38	0.38	4–5	53	14.78	1.35	13–19
5	48	4.81	0.35	4–5.5	46	16.71	1.18	14.5–19.5
6	44	5.22	0.44	4.5–6	47	19.33	1.54	17–23
7	45	5.73	0.43	5–7	42	21.67	1.62	19–25
8	42	6.23	0.44	5.5–7	42	23.89	1.36	21.5–26.5
9	37	6.55	0.47	6–7.5	37	26.69	1.74	23.5–29.5
10	39	7.02	0.51	6–8	38	28.32	1.63	26–31
11	31	7.37	0.48	6.5–8	31	30.34	1.62	28–34
12	33	7.91	0.42	7–9	34	31.80	1.39	29–35
13	26	8.15	0.56	7–9	26	33.44	1.62	30–37
14	26	8.60	0.53	7–9	26	34.85	1.08	32–36.5
15	20	8.85	0.56	8–10	20	35.48	0.91	34–37.5
16	8	9.69	0.37	9–10	8	36.38	1.22	34–38

days, have carpometacarpi that average 71% adult length. Tarsometatarsi at age 10 days average a similar 74% adult length. Young Scrub Jays cannot fly for many days after leaving the nest, but this may be caused by factors other than retarded growth of wing bones, such as slow development of muscles and feathers.

TABLE 3

AGE AND MEAN MEASUREMENTS (MM) OF FLORIDA SCRUB JAYS

Age in months	N	Beak from nostril	Tarsus	Primary no. 7	Deck
0.5	20	**8.9 ± 0.56^{S}	**35.5 ± 0.91	**34.1 ± 1.79	**10.9 ± 3.09
0.5–1	16	**9.8 ± 0.52	36.6 ± 1.21	**42.1 ± 5.60	**20.2 ± 7.92
1–2	9–13	15.3 ± 0.56	36.7 ± 1.32	**82.2 ± 1.77	*124.6 ± 6.37
3–4	27–30	**15.5 ± 0.86	36.7 ± 1.34	84.8 ± 2.20	129.4 ± 4.93^{M}
6–12	10–11	17.0 ± 1.15	37.0 ± 1.52	**83.7 ± 2.72^{W}	**128.9 ± 5.58^{D}
24+	36–56	17.5 ± 0.95	37.7 ± 1.36	87.5 ± 2.86^{D}	134.9 ± 5.56^{D}

S = means followed by 1 standard deviation.
Asterisks mark each mean that is significantly different from the mean immediately beneath it (*t*-test).
W = wear may have caused reduced length from previous age class.
D = different feathers from those measured for previous age category.
M = molt of juvenal decks begins at about age 3 months.

Weight.—The growth measurement analyzed in greatest detail is weight. As a base for comparisons the weight of adult-plumaged jays is described first. An adult-plumaged Florida Scrub Jay weighs 79.2 g (s.d. = 4.86). The 60 weights chosen for this determination are of 5 live jays of each sex for 6 bimonthly periods (Dec.–Jan., etc.). All individuals chosen were at least 2 years old and appeared to be in good health. The sample range (65.6–92.0 g) encompasses the 283 live weights available for Florida Scrub Jays 2 years old and older. Variation in weight with sex in Scrub Jays was shown by Pitelka (1951) for various of the western races, but he had only 3 weights for the Florida race. The 30 males I used to determine "adult" weight averaged 81.7 g (s.d. = 4.09, range 74.1–92.0), the females 76.7 g (s.d. = 4.25, range 65.6–84.5). The weight difference between sexes is highly significant (t = 4.67). Seasonal variation in weight of adult-plumaged jays, sexes combined, is graphed at bimonthly intervals (Fig. 2); no significant differences among the 6 samples were found.

Bent (1946) describes the color, shape, and size of Florida Scrub Jay eggs, but gives no weights. The mean size of 26 eggs laid in my study tract in 1973 and 1975 (27.5 × 20.5 mm) is similar to that for Bent's sample of 46 eggs taken from various localities in Florida prior to 1946 (27.5 × 20.3 mm). The weights of 32 fresh eggs, all measured within 1 day after laying in 1973, averaged 5.81 g (s.d. = 0.66, range 4.1–7.1); the weights of 27 eggs in the process of hatching (not necessarily the same eggs) averaged 5.03 g (s.d. = 0.55, range 4.3–6.2). For these samples weight loss from the time of laying to the time of hatching averaged 13.3%. Eight eggs weighed when fresh and also during hatching sustained weight losses ranging from 6.8 to 18.9%, with a mean loss of 12.8%, which is similar to the 13.3% registered for the larger but less controlled sample.

According to Nice (1943:74) fresh eggs weigh 8–12% of the adult female in passerines weighing up to 135 g. Nice deleted from her summary corvids weighing over 135 g, which had lesser percentages (2.5–5%). For Florida Scrub Jays, fresh eggs weigh 7.6% of adult females. In the Piñon Jay fresh eggs ($\bar{x}$ = 6.65) weigh 6.4% of adults ($\bar{x}$ = 103.3), both sexes included (calculated from Bateman and Balda 1973). Perhaps corvid eggs tend to constitute a smaller percentage of adult weight regardless of size. Four unfed hatchlings averaged 4.19 g (range 3.6–4.5). The weight of additional unfed hatchlings was estimated by subtracting the mean weight of moist empty shells, taken from eggs that failed to hatch, from the mean weight of hatching eggs. Seven fresh empty shells averaged 0.5 g (range 0.4–0.7), and the hatching eggs averaged 5.03 g, giving an estimated average value of 4.53 g. At 78% the weight of a fresh egg (5.81 g), hatchling Florida Scrub Jays are within the range listed for certain other passerines: *Lanius ludovicianus*

TABLE 4
WEIGHTS OF NESTLING FLORIDA SCRUB JAYS

Age in days	N	Weight (g)			Age in days	N	Weight (g)		
		x̄	S.D.	Range			x̄	S.D.	Range
0	50	4.82	0.73	3.5–6.5	9	37	38.22	4.67	28.4–49.0
1	55	6.83	1.01	5.4–9.2	10	40	41.97	4.86	32.6–55.6
2	55	9.33	1.42	7.3–13.9	11	32	47.26	5.79	36.7–59.0
3	58	12.77	2.55	9.1–23.0	12	33	51.18	4.39	41.5–60.3
4	57	16.03	2.47	12.1–24.6	13	26	55.93	4.87	47.0–64.0
5	45	19.61	2.87	14.3–25.4	14	26	56.55	4.42	49.0–68.0
6	44	23.80	3.46	17.3–31.2	15	20	59.62	4.89	51.0–67.0
7	42	29.03	4.11	21.4–35.2	16	8	59.75	2.25	57.0–64.0
8	46	32.77	4.11	24.4–40.6					

73–75% (Miller 1931), *Molothrus ater* and *Quiscalus quiscula* 73% (Wetherbee and Wetherbee 1961) and *Agelaius phoeniceus* 79% (Holcomb and Twiest 1968). The 95% figure obtained for Piñon Jays is suspect as pointed out by the authors. Hatchling Florida Scrub Jays weigh 6% of an adult's weight, which also is within the range for certain other passerines at 6–8% (Nice 1943) including the Piñon Jay (Bateman and Balda 1973).

The weight data for nestlings obtained in 1973 are summarized in Table 4 and graphed in Fig. 1. The day 0 weights used were taken almost entirely from nestlings that had received food before weighing. These compilations obscure the considerable variation that exists in the number of helpers and nestlings that a given pair may have. These important variables are discussed below.

Ricklefs (1968) found that growth for 2 corvid species was best described by the logistic equation:

$$W = \frac{A}{1 + e^{-K(t_w - t_o)}}$$

where W is the weight of the bird in grams at the age t_w (in days), A is the asymptote of weight (g) approached by nestlings, e is the base of natural logarithms, K is a constant proportional to the specific rate of growth, and t_o is the age in days at the point of inflection on the growth curve. The procedures outlined by Ricklefs (1967) were used by Bateman and Balda (1973) and in this study with similar results. For the Florida Scrub Jay, A is 60.0 (78.9 for the Piñon Jay). The age at which half of A is attained (t_o) is 8.2 days (7.6 for the Piñon Jay). The overall growth rate index (K) for the Florida Scrub Jay (0.335) is similar to that for the Piñon Jay (0.328)

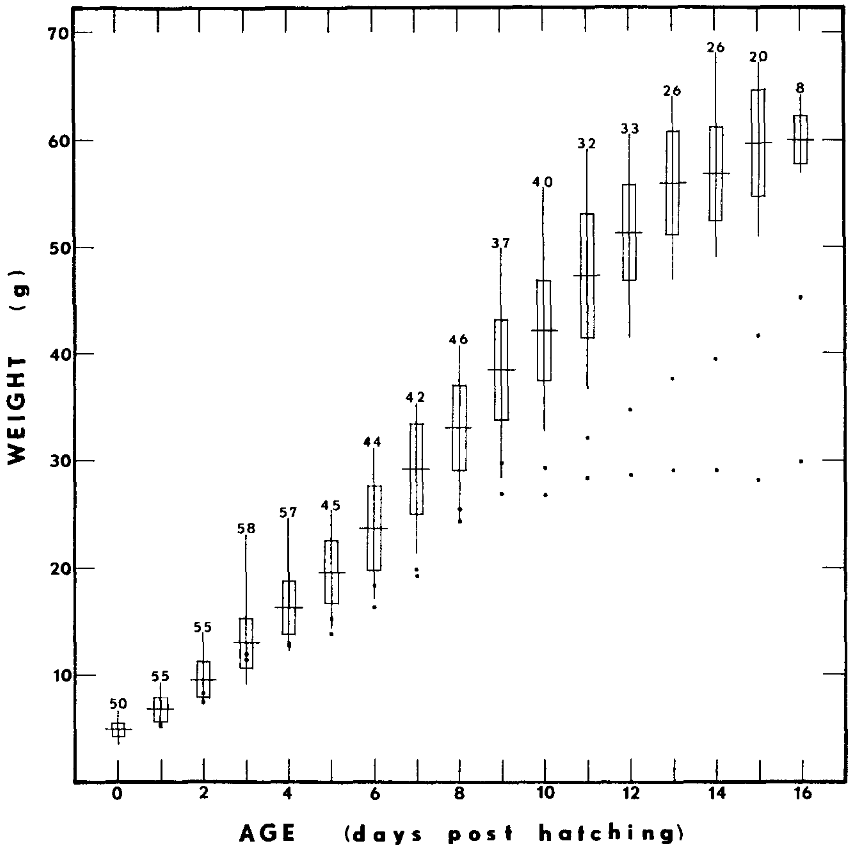

FIG. 1. Weights of nestling Florida Scrub Jays. In the diagram the single vertical line represents the range of observations, the cross line the mean, the open column 1 standard deviation, and the figure atop each vertical line the sample size. Below each mean, starting with day 1, are 2 points which represent the weights of 2 starving siblings.

and the magpie *Pica pica* (0.332), but larger than that for the crow *Corvus brachyrhynchos* (0.172), a large, slow growing passerine.

An inverse measure of the overall rate of nestling growth (K) is the time required to grow from 10% to 90% (t_{10-90}) of the asymptote (Ricklefs 1968). Based on Ricklefs' regression equation of t_{10-90} on body size, the crow grows more slowly than expected (observed = 25.5 days, expected = 21.5 days), the magpie more rapidly (observed = 13.3, expected = 17.7), the Piñon Jay essentially as expected (observed = 13.4, expected = 13.3), and the Scrub Jay slightly slower (observed = 13.1, expected= 12.3).

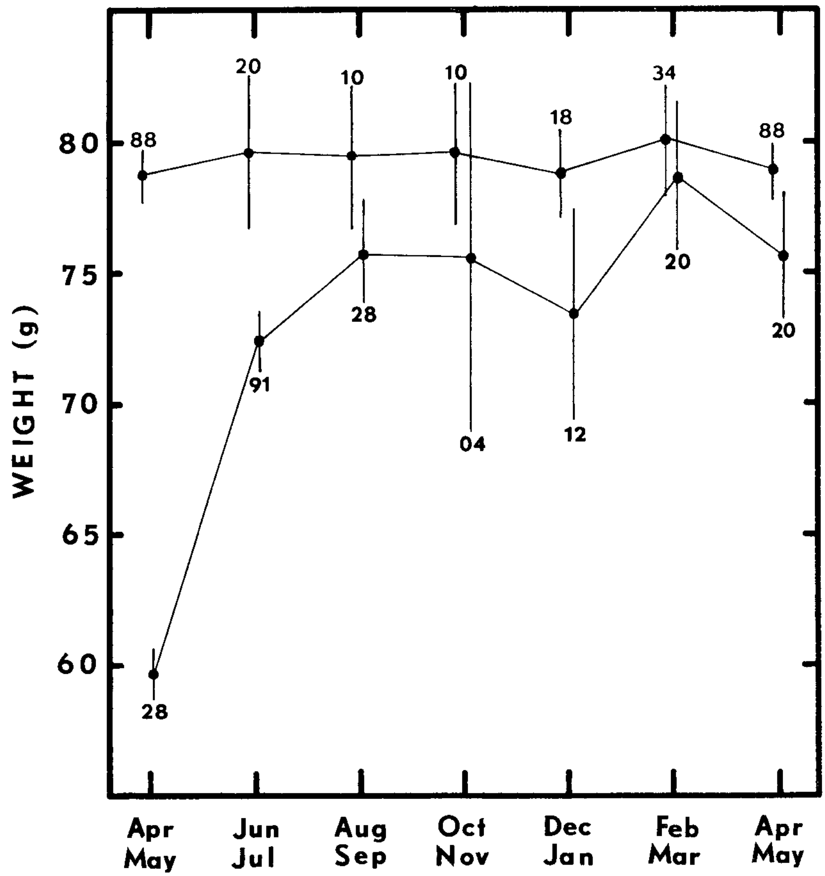

FIG. 2. Annual fluctuation in weights of "adult" and fledgling Florida Scrub Jays. The lines connect the bimonthly means for "adults" (upper) and fledglings (lower). The vertical bars represent 95% confidence levels. The figures denote the bimonthly sample sizes for adults (above the lines) and fledglings (below the lines). Fledglings were weighed from day of departure from the nest (left side April–May sample) through 1 year.

The ratio between the asymptote and adult weight describes development at fledging. The Florida Scrub Jay at 0.76 is similar to the Piñon Jay at 0.79 (Bateman and Balda 1973), and below the values obtained for 42 of 56 other passerines (Ricklefs 1968, Table 2, R value). Low values correlate with adult foraging and fledgling escape tactics, namely moving about on the ground in search of food and eluding predators by running. An additional factor may be the location of the nest, with early fledging of species whose

TABLE 5

WEIGHTS AND THE FEEDER INDEX FOR NESTLING FLORIDA SCRUB JAYS

	Feeder index 0.5–1.4 Weight (g)				Feeder index 1.5–3.0 Weight (g)		
Age in days	N	x̄	S.D.		N	x̄	S.D.
0	39	4.74	0.66		11	5.09	0.91
1	47	6.78	0.98		8	7.13	1.21
2	45	9.34	1.48		10	9.34	1.18
3	49	12.62	2.67		9	13.63	1.62
4	47	15.72	2.43	*	10	17.51	2.21
5	36	18.90	2.84	*	9	21.39	2.59
6	35	23.16	3.15	*	9	26.32	3.62
7	35	28.58	3.96		7	31.30	4.42
8	39	32.24	3.90	*	7	35.70	4.33
9	31	37.51	4.43	*	6	41.90	4.47
10	34	41.02	4.31	**	6	47.35	4.51
11	26	45.98	5.21	**	6	52.83	5.16
12	27	50.24	4.15	**	6	55.42	2.76
13	13	54.60	4.66	**	6	60.35	2.31
14	13	55.15	3.62	**	6	61.20	3.72
15	14	58.29	4.78		6	62.72	3.88

* and ** indicate significant differences at the .05 and .01% level, respectively.

nests are more accessible to predators. Scrub Jays do not achieve adult weight for many months post fledging (Fig. 2).

Weights of fledgling and adult-plumaged jays are plotted at bimonthly intervals for 1 year (Fig. 2). The fledgling weights include only those of jays up through 1 year of age from the 1973 and 1974 year classes. The sex of many of these fledglings was unknown, however at age 1 year the sex ratio of Florida Scrub Jays seems to be equal (Woolfenden 1975), and therefore all available weights were used.

Covariance analyses ($\alpha = 0.05$) of the data graphed in Fig. 2 reveal the following relationships. Weights of "adults" from May through August–September are statistically indistinguishable from the weights of "adults" taken from October–November through the following April–May; thus all "adults" are treated as 1 unit in the comparisons with fledglings. The weights of fledglings taken from time of fledging in May through August–September are neither coincident nor parallel with the weights of fledglings taken from October–November through the following April–May, and the same is true of their relationship to the weights of all "adults." The weights of fledglings taken from October–November through the following April–May also are non-coincident ($p < 0.05$) with the weights of all "adults," but they are

TABLE 6

WEIGHTS AND THE FEEDER INDEX FOR 130 DAY 11 NESTLING FLORIDA SCRUB JAYS

			Weight (g)		
Year	Feeder index	N	$\bar{x}$	S.D.	Range
1973	0.5–1.4	26	**45.98	5.21	36.7–55.0
	1.5–3.0	6	52.83	5.16	47.1–59.0
1974	0.4–1.4	11	*38.95	7.13	29.6–49.2
	1.5–2.7	5	48.10	5.05	40.6–54.5
1975	0.5–1.4	68	*43.49	7.44	24.6–56.2
	1.5–2.0	14	48.32	5.22	39.4–58.4

Asterisks (*) mark each mean that is significantly different from the mean immediately beneath it (*t*-test).

parallel. These analyses support the conclusion that after gaining rapidly from fledging until August–September, the young jays level off at a weight below that of "adults." Inspection of the bimonthly samples (Fig. 2) reveals that between October–November and the following April–May, fluctuations in the weights of "adults" and fledglings tend to be parallel. The only bimonthly change that is significant is for fledglings between December–January and February–March ($t = 2.36$); however the concomitant gains and losses by the 2 age-classes suggest that the changes may be real.

In 1973 significant differences in weight existed between chicks with low (0.5–1.4) and high (1.5–3.0) feeder indexes almost daily from day 4 to day 14. Significant differences apparently occur most years as evidenced by weights of day 11 chicks for 3 consecutive years (Table 6), including 1974 when the feeder index ranged from 0.4 to 2.7 and 1975 when the range was 0.5 to 2.0. Day 11 was chosen for time of weighing because it is late enough in the nestling cycle for differences in weight to have developed, but early enough that handling the young does not cause early fledging. Day 11 also is a convenient age for banding. Few other weight data useful for comparing years were obtained, and none was analyzed.

MORTALITY FACTORS

Though difficult to measure, starvation of nestlings seems a minor cause of death in Florida Scrub Jays. Based on once-daily or less frequent visits to nests during the 6 years 1970–1975, 33 of 342 nestlings (10%) disappeared from broods known to have had a continued existence. Such gradual attrition of broods probably includes almost all nestling starvation, but also includes deaths caused by genetic defects, diseases (including parasitism), and some predation. Thus starvation apparently kills considerably less than 10% of Florida Scrub Jay nestlings.

As a measure of starvation relative to brood size, gradual disappearance of young was measured only from nests without helpers and with broods of different sizes. For unassisted pairs with broods of 2 (n = 11), 3 (n = 25), and 4 (n = 15) nestlings, the number of young lost from continuing broods is similar at 18, 21, and 17%, respectively. As the feeder index decreases from 1.0 to 0.5 for these unassisted pairs with 2 versus 4 nestlings, this independent analysis suggests that food provisioning for nestlings is not a factor critical to reproductive success in the Florida Scrub Jay. However, food availability probably has selected for clutch size which averages only 3.4 (Woolfenden 1973).

During 7 years of watching nests, 2 breeding attempts have produced grossly underweight broods, and both of them fledged. In 1973 an unassisted pair fledged an underweight brood of 2. The young were far below normal weight a few days after hatching and soon appeared weak and sick. Their weights are plotted separately in Fig. 1. Growth of extremities, as well as weight, were retarded. At age 15 days both young were below the minimum recorded for all 4 linear measurements taken on heavier and relatively healthy young (Tables 1 and 2), and measured as follows: primary 7, 24 and 18.5 mm, deck, 3 and 0 mm, beak, 7.5 and 7 mm, and tarsus 32 and 29 mm, and weight 41.5 g and 28.0 g, respectively. These young fledged during days 21 and 20, respectively, and the lighter weight individual in all probability died within a few days. The heavier fledgling died at age 99 days, at which time he weighed only 49.6 g. However on day 82 he weighed 73.1 g, which is almost normal for that age (see Fig. 2). A heavy helminth burden may have contributed to its death (see Kinsella 1974, specimen GEW 4804).

The male (-WWS) of this breeding pair appeared to be a poor provider who seemed to spend an inordinate amount of time perched near his nest. Three years earlier, as a semi-independent fledgling in his natal territory human occupants of a nearby cabin provided the jays with a bountiful supply of peanuts. At that time I noted that this bird rarely foraged for animal food as do other young fledglings; possibly he never gained the foraging efficiency or drive necessary for feeding young.

In 1974 a case of bigamy resulted in the fledging of a brood of 2 underweight and sickly young, both of which died within days of fledging. Details, including weights of the nestlings, are given by Woolfenden (1976).

In both these instances it seems that abnormal behavior of the breeding male resulted in failure to provide sufficient nourishment to young, even though the feeder indexes at 0.5 were not abnormally low. Under normal circumstances breeding female Scrub Jays spend a large percentage of their time at the nest (unpubl. data), especially early in the nestling cycle. Perhaps this general tendency prevented these 2 females from leaving their nests to forage and thereby compensate for the inadequacies of their mates. The point of interest here is that even when breeders exhibit abnormal behavior resulting in grossly undernourished nestlings, fledging can occur in the absence of predation.

In his analysis of 6 passerine species, Ricklefs (1969) identified only a few causes for nestling loss other than starvation and predation. Two of these, desertion and weather, are easily identified for Florida Scrub Jays and are known to be rare. By elimination, predation accounts for about 80% of all nestling losses in the population, a percentage that is considerably higher than the 66% tallied for the other 6 species. The high rate of nestling predation sustained by Florida Scrub Jays probably selects strongly for a breeding regime that reduces such losses.

SURVIVAL

Previously, survival through the first year of life was compared to adult mortality (Woolfenden 1973), based on a sample of 143 young from 4 year classes (1969–1972). Now, with a sample of 269 young from 6 year classes, 1970–1975 (the 1969 sample which is small is deleted to reduce chance of bias), and many weight data, it is possible to examine survival as related to nestling weight, the feeder index, and the presence of helpers.

Table 7 summarizes information on survival to feeding independence, which virtually always is accomplished by August at age three months, for 115 of the 130 young whose weights as nestlings are shown in Table 6. No differences in survival are evident among the various weight groups. Perhaps with very large samples the lightest-weight fledglings could be shown to be faring less well, and the same might be true for the heaviest young. However, neither the Mann-Whitney U-test nor the Wilcoxon 2-sample test demonstrated significance with the present sample.

The feeder index can be used in an indirect method of comparing weight and survival. As shown in Tables 5 and 6, nestlings from families with a high feeder index (1.5–3.0) weigh more than nestlings from families with a low feeder index (0.4–1.4). Even though weights were obtained for only a small portion of the young jays that have been banded and censused, the feeder index is known for virtually all. Thus the sample of young whose post-fledging survival to independence was monitored more than doubled (115 to 267) when the feeder index was used as an indication of high or low weight. The number of year classes available for testing also increases, from 3 (1973–1975) to 6 (1970–1975). The data are arranged in Table 8, and again no cause-and-effect relationship is evident; indeed survival plotted against the

TABLE 7

POST-FLEDGING SURVIVAL OF 115 FLORIDA SCRUB JAYS ARRANGED BY DAY 11 WEIGHT

Weight (g) on Day 11	Total fledglings	No. of independent young	Percent surviving
55–60	6	2	33
50–54	24	13	54
45–49	42	21	50
40–44	22	9	41
35–39	10	6	60
30–34	6	3	50
25–29	5	2	40

feeder index yields a straight, horizontal line. These data support the premise that weight of nestlings has little effect on their later survival. Snow (1958) came to similar conclusions from his study of Blackbirds (*Turdus merula*). A regression analysis between feeder index and weight was not made because recent field work shows that merely counting the number of jays bringing food to a nest is an oversimplification in that amount of food brought varies with age and sex of individual jays (Stallcup and Woolfenden in press).

Florida Scrub Jay helpers do help, and they do so by increasing the reproductive output of breeders, usually close kin, with whom they affiliate (Woolfenden 1975). This conclusion, based on data from 1969 through 1973, is further supported by similar analyses of unpublished data obtained in 1974

TABLE 8

POST-FLEDGING SURVIVAL OF 267 FLORIDA SCRUB JAYS ARRANGED BY THE FEEDER INDEX

Feeder index	Total fledglings	No. of independent young	Percent surviving
3.0	1	0	0
2.7	3	0	0
2.5	3	3	100
2.3	2	2	100
2.0	18	11	61
1.7	17	8	47
1.5	14	5	36
1.3	20	12	60
1.0	73	34	47
0.8	37	20	54
0.7	44	24	55
0.5	35	17	49

TABLE 9

POST-FLEDGING SURVIVAL OF 269 FLORIDA SCRUB JAYS FROM FAMILIES WITH AND WITHOUT HELPERS

Helper status	Feeder index	Total nestlings	Percent fledglings	Percent independent young
No helpers	2.0	6	50	33
	1.0	30	57	35
	0.7	87	54	55
	0.7–2.0	123	54	49
Helpers	2.0	26	58	67
	1.0	77	73	50
	0.7	43	79	53
	0.7–2.0	146	72	53

and 1975. But the help helpers provide the young has little to do with food needed and food supplied (Tables 7–8). To further substantiate this phenomenon, I stabilized the weight variable by measuring survival of young jays only in families with the same feeder index, some of which had helpers, some of which did not (Table 9), and the difference between production of fledglings by families with and without helpers is highly significant (χ^2 = 17.9). Survival of fledglings to feeding independence also is greater for the young from families with helpers although the differences are significant for only 2 of the feeder index categories (2.0 and 1.0), and not for the third (0.7) or for all 3 combined.

As a separate analysis, loss of clutches was measured for pairs without and with helpers with similar results: 34% of 93 nesting attempts by families without helpers were destroyed prior to hatching, but only 23% of 120 by pairs with helpers. The difference is significant (χ^2 = 5.7). As eggs do not starve, this provides further evidence in opposition to the hypothesis that food provided relative to food needed limits Florida Scrub Jay reproductive success.

A question that remains is: How do helpers help increase reproductive output if it is not by means of providing the food necessary for survival of young? In the preceding section on nestling mortality, predation was identified as the factor responsible for about 80% of all nest losses. Suspected nest predators include Fish Crows (*Corvus ossifragus*), possibly Blue Jays (*Cyanocitta cristata*), certain snakes and mammals, and Scrub Jays themselves (Woolfenden 1973, 1975). Scrub Jays have an elaborate active nest defense that includes scolding, plumage displays, mobbing, and outright attack, all of which suggest these jays are capable of dissuading certain nest predators. Thus I suggest the major way that Florida Scrub Jay helpers help is by decreasing predation on the nests containing eggs or nestlings, and to some extent on the scattered fledglings, of the breeders with which they affiliate.

CONCLUSIONS

Growth of nestling Florida Scrub Jays seems typical of passerines their size. Minor developmental features common to both Piñon and Scrub jays, which Bateman and Balda (1973) consider adaptive for breeding during cold weather by Piñon Jays, seem adaptive for breeding in a hot sunny climate by Florida Scrub Jays. Thus dark skin pigmentation and the more rapid development of dorsal feathers than those of the venter may help shield nestlings from harmful quantities of ultraviolet light. At fledging Scrub Jay young are less developed than most passerines studied thus far (Ricklefs 1968), and although comparative data are few, post-fledging growth seems retarded, as evidenced by the failure of young to attain adult weight by the end of a year. The social organization of the population probably allows for gradual growth, and indeed it may even cause it. If an advantage exists for gradual growth, the security of a defended natal territory may permit it. As an alternative hypothesis, intrafamilial dominance hierarchies relegate fledglings to subordinate positions (Woolfenden and Fitzpatrick 1977), which may suppress their gaining weight. It remains to be established whether or not these hierarchies result in higher survival of birds of particular weights.

Most Florida Scrub Jay nests fail (Woolfenden 1973), but rarely because of desertion or weather. Starvation accounts for less than 10% of all nestling losses while predation apparently accounts for over 80%. Young fed by relatively more feeders are heavier, but weight and the feeder index do not affect post-fledging survival. However, survival to fledging is related directly to the existence of helpers (Woolfenden 1975 and Table 9). Preliminary observations indicate the amount of help helpers provide varies with sex and age; therefore more refined measures of success relative to number of helpers are omitted intentionally. It is postulated that helpers assist breeders by reducing nest predation. The possibility that group breeding results in direct advantages to the breeders and the helpers is currently under investigation.

SUMMARY

Growth of young was measured in a marked population of Florida Scrub Jays that has been censused from 1969 to the present. Data were gathered mostly in 1973 when samples ranged up to 59 nestlings, which were the reproductive efforts of 28 pairs.

Fresh eggs weigh 5.8 g, 7.6% of adult female weight, and lose about 13% of their weight during incubation. Newly hatched, unfed young weigh about 4.5 g, about 78% of a fresh egg. Based on growth curve computations, nestling growth is half completed at 8.2 days. The overall growth rate index of 0.335 is similar to that of Piñon Jays, and the young

grow only slightly slower than expected for their body size. Development at fledging lags behind most passerines thus far measured, as is true also of Piñon Jays. Florida Scrub Jays do not attain "adult" weight during the first year. Growth of certain extremities also requires many months. Fluctuations in fledgling weights parallel those of "adults" from fall to early spring.

Desertion and weather rarely cause nesting failure, and starvation of nestlings accounts for less than 10% of nestling losses. Predation is the major factor; it accounts for over 80% of all nestling losses.

Breeding pairs with helpers produce more young, especially fledglings, than do unassisted pairs. Nestlings fed by relatively more feeders are heavier, but survival as fledglings does not correlate with nestling weight or the feeder index. Even nestlings half normal weight at day 11 appear to survive as fledglings as well as do heavier birds. Decreasing predation, especially on nest contents, is proposed as the major way that helpers increase reproduction. Elaborate active nest defense by breeders and helpers supports the suggestion. The suspected predators they may sometimes dissuade are certain snakes, Fish Crows, Blue Jays and Scrub Jay cannibals.

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REQUEST FOR ASSISTANCE

Vulture sightings.—Sightings of and information about Turkey Vultures tagged with blue or orange streamers, each with a white letter and a one or two digit number, would be appreciated. The tags are about 3″ × 6″ and are fastened to the patagium with a numbered cattle ear tag. Birds are tagged on either the right or left wing. The tags are on both the dorsal and ventral surfaces of the wing. Data requested include: tag number, tag on left or right wing, date, time and place of sighting, activity of the bird and its proximity to other birds. I am particularly interested in tagged birds seen mating or in the nest. An opportunity to tag nestlings of tagged birds would be invaluable. Please send sighting data to: Bird Banding Laboratory, Office of Migratory Bird Management, Fish and Wildlife Service, Laurel, MD 20811 and/or Sheila Parness Gaby, 6832 S. W. 68 St., S. Miami, FL 33143.