GROWTH, DEVELOPMENT, AND FOOD HABITS OF YOUNG PIÑON JAYS

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Despite numerous reports of growth and early development in a variety of passerines (Banks, 1959; Anderson and Anderson, 1961; Willson, 1966; Ricklefs, 1967a; Holcomb and Twiest, 1968) relatively few such studies have dealt with members of the family Corvidae. Parmalee (1952) describes the growth and development of *Corvus brachyrhynchos*, and Pitelka (1945) gives valuable information on molt sequences and other age specific characteristics of early plumages in the genus *Aphelocoma*. Mewaldt (1956) published data on growth and development of Clark's Nutcracker (*Nucifraga columbiana*) and Crossin (1967) briefly described development of the Tufted Jay (*Cyanocorax dickeyi*) during the nestling and early postfledging period. Ricklefs (1967b, 1968a, 1968b) stresses the importance of discovering causes underlying the existing diversity of growth patterns in birds. He feels that comparative studies of growth will reveal much about the ecology of some species.

This study provides quantitative and qualitative information regarding growth of one of the more unusual corvids. The Piñon Jay (*Gymnorhinus cyanocephalus*), a highly social species, is one of the earliest nesting passerines in the north temperate region. Studies of young born during periods of inclement weather should reveal some factors influencing growth rates under adverse environmental conditions. The high degree of sociality of this species may contribute significantly to the pattern of growth and development of the young.

METHODS

This report describes the growth and development of young from a flock of about 250 Piñon Jays nesting in an area of the ponderosa pine forest 10 miles northeast of Flagstaff, Arizona. Studies of the annual cycle and social behavior of this species initiated in February 1968 have continued through the 1971 breeding season (Balda and Bateman, 1971). Growth and development of young were of major concern during the first 3 years of study.

Temperature data were obtained by a hygrothermograph on the study area. Precipitation (Table 1) in the form of snowfall was measured at Flagstaff Pulliam Airport, 13 miles southwest of the nesting grounds at a comparable elevation. Differences in amount of snow received at the two areas are relatively minor.

From February through June nests containing eggs and/or young were checked as often as prudent consideration of the parent birds allowed. The study area was normally visited from two to five times a week. It was not always possible to examine all nests at a given visit because of the large number of contemporaneously active nests, but we do have almost daily records of growth for some individuals during their nestling periods.

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TABLE 1

TEMPERATURE (°C) AND SNOWFALL (CM) FOR THE REPRODUCTIVE PERIOD

	Mean daily high		Mean daily		Mean daily low		Snowfall	
	1968	1969	1968	1969	1968	1969	1968	1969
Feb.	9.0	6.7	2.3	0.2	-4.3	-6.3	23.6	106.9
Mar.	12.4	8.2	3.7	-0.1	-4.9	-7.2	25.7	110.7
Apr.	11.5	15.2	5.7	6.4	-2.9	-2.4	57.7	1.5
May	20.6	20.6	12.2	12.8	2.2	2.8	5.1	11.7
June	29.4	23.9	18.3	16.1	7.2	7.2	0.0	0.0

Because of their small size newly hatched young were not banded, and early growth records of individuals in a given nest were not kept separately for the first week of life if the birds were of equal ages. If the young of a single brood hatched on different days, the larger birds were considerd to be older (the validity of this assumption was borne out by ink-marking young of several broods).

At about 1 week of age each nestling was fitted with a U. S. Fish and Wildlife Service band and one or more plastic color bands. The latter were closed with a few drops of acetone which made a tight seal at the overlapping edges. Before using acetone we found several color bands beneath nests; presumably these bands were removed by the parents. Growth records of individuals were kept separately after banding.

Nestlings were weighed to the nearest 0.1 g on a triple beam balance with an animal subject box. In addition the lengths of the distalmost remex (P–10) and outer rectrix (R–6) were measured with a transparent millimeter rule inserted along the medial surface of the feather shaft until it abutted the flesh at the base of the feather.

Observations of a more subjective nature included extent of eye opening, coloration of the beak, degree of skin pigmentation, and general behavior of the young. Generally birds were handled for less than 10 minutes. A series of nestlings of various ages preserved in alcohol provided data on bill size, tarsometatarsal length, and toe span. Notes on growth and molt were also made on 11 young kept in captivity for up to 2 years.

During the spring of 1970, 24 nestlings of 6 different broods were collared with short lengths of pipe cleaner to prevent their swallowing food, as described by Orians (1966). Nests were checked at approximately hourly intervals and food items found in the throats were removed and placed in individually labeled vials of 60 percent isopropyl alcohol. Food taken from each individual was kept separately and considered a single sample.

LENGTH OF INCUBATION PERIOD

Events leading up to and during the incubation period are more completely discussed elsewhere (Balda and Bateman, 1971, 1972).

Our observations show the incubation period as defined by Nice (1954) to be 17 days, as Ligon (1971) also found in New Mexico. We were able to determine exactly the dates of oviposition and hatching of 66 eggs that we numbered sequentially as laid in 20 nests (Table 2).

TABLE 2
THE INTERVAL FROM DATE OF FINAL OVIPOSITION TO HATCHING FOR 66 EGGS FROM 20 NESTS[1]

Interval (days)	Clutch size				Totals
	2	3	4	5	
15				8	8
16		2	11	4	17
17	4	7	14	14	39
18			1	1	2

[1] Note: not all eggs in these nests hatched.

On many occasions, several of which are not shown in Table 2 because dates of oviposition were not known, eggs of a single clutch hatched over a 2- or 3-day interval. We often saw females sitting on nests with incomplete clutches, even during warm afternoons. It was not possible to determine whether they were applying enough heat to cause development, but our indirect evidence led us to believe that they were. In about half of the 5-egg clutches in Table 2, for example, 3 eggs hatched on the 15th day and the other 2 on the next successive days, suggesting that the females started incubating with the laying of the third egg. In clutches of four eggs about half the females also apparently began to incubate with the third egg (three clutches). In three nests with clutches of three only one bird began incubating before completing the clutch. Eggs of other three-egg clutches usually hatched on the same day. During the 1971 nesting season, a particularly dry year, a female with a clutch of five began to sit continuously the day she laid the second egg. Eggs in this nest presumably would have hatched over a 4-day interval, but the female deserted before they hatched.

Asynchronous hatching is known in many other birds including the Common Swift (*Apus apus*) and crows (*Corvus* spp.) (Lack, 1954), American Goldfinch (*Spinus tristis*) (Berger, 1968), Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) (Willson, 1966), and Roadrunner (*Geococcyx californianus*) (Ohmart, 1972). According to Lack (1954) asynchronous hatching is an advantageous adaptation of species with a highly variable food supply. As Piñon Jays normally do not start incubating before depositing the third egg, this may be the most common number of young reared in late winter and early spring. The fourth and fifth young of a brood may be "bonus babies" and have best chances of survival in optimum years when food is unusually plentiful. The fact that not all females with clutches of five begin incubating before laying the last egg indicates that asynchronous hatching of larger broods is not an inflexible characteristic of the species, though variability in hatching times is positively correlated with clutch size (Table 2).

In Clark's Nutcracker, another early nester, Mewaldt (1948) noted that the parent birds covered the eggs as soon as oviposition began, yet all eggs of a clutch usually hatched the same day. He later (1956) suggested that the heat applied prior to final oviposition was merely enough to keep the eggs from freezing, and "true" incubation began after the clutch was complete.

Temperatures at our study area (Table 1) were similar to those Mewaldt (1948, 1956) recorded, yet Piñon Jays did not normally begin to maintain a vigil on the nest with the laying of the first egg. In 1970 many eggs not being incubated cracked from freezing during early nesting attempts.

GENERAL DEVELOPMENT AND BEHAVIOR

Days 0-1.—At hatching the young were pink-skinned (*contra* Bent, 1946) with no obvious darker pigmentation. Pterylae were discernible as roughened areas and tiny transparent bristles were visible at the sites that would later bear rectrices, but true neossoptiles were totally absent. The beak was yellowish-pink and bore a whitish egg tooth at the tip of the upper mandible. Culmen length was about 7.5 mm and the width across the commissural points was approximately 10.5 mm. The inner lining of the mouth was a bright salmon red. The ventral abdominal wall was thin and the viscera clearly visible. The tarsometatarsus was about 11 mm in length and the toe span 13.1 mm. The feet and legs seemingly performed no important function at this time.

The nestlings were very weak and unable to orient their bodies into any typical position. They lay on their backs or sides (usually) at this time. The neck was often flexed ventrally at rest and the young moved about weakly when disturbed and could squeak softly.

Days 7-8.—At this age the young were heavily pigmented, the skin throughout having a dark purplish-blue hue most pronounced in the pterylae. Even though pterylae were obvious at this time the birds were essentially naked, as feathers were still sheathed and short. Primaries were quills of more or less equal length, the outermost (P-10) measuring about 4 mm. The marginal coverts of the alar tract projected through the skin. The greater and middle secondary coverts were about 4 mm and 2 mm respectively. Feathers of the spinal tract were mere pins, being longest (ca. 3 mm) in the dorsal region. Ventrally the birds appeared even more naked. The rectrices were still represented only as tiny whitish brushes. The eyes began to open most often by day 7 ($\bar{x} = 7.1$, n

= 27) and in all but a single case had started to do so by day 8. They were often completely open by day 8 or 9 and were dull blue-gray in color. Culmen length had doubled over its size at hatching, being about 16 mm, and the fleshy flaps of skin at the commissural angles were still large and tinted a pale yellow. The commissural width was 16–17 mm at this time. The mouth lining was bright orange-red. The egg tooth was evident as a prominent white tubercle. The hind limbs had grown rapidly assuming an important function as supportive structures during the begging and feeding activities. The length of the tarsometatarsus had more than doubled since hatching, measuring approximately 29 mm. The toe span likewise had increased greatly, due in considerable part to claw growth, and measured about 31 mm.

The development of the hind limbs and the opening of the eyes now enabled the birds to become more alert and active beggars. Prior to this time vibrations associated with our tree climbing usually elicited begging behavior; now the birds were becoming responsive to visual cues and were much more vociferous and active in their food soliciting. When a hand was held above them they stretched upward, supporting themselves on the prostrate tarsometatarsus, and flapped their wings weakly while emitting loud begging squeaks and harsh squawks.

Days 14-15.—The birds appeared in dorsal view to be fairly well-feathered. The outermost primary measured approximately 24 mm and was sheathed basally for about half of its length. The secondaries were growing rapidly and the birds used their wings for balancing when perched on one's finger. There were large bare areas on the undersides of the wings. The tail was markedly stubby and the rectrices were sheathed for more than half their lengths. In some cases the under and upper tail coverts equalled or exceeded the rectrices in length. Ventrally, particularly in the abdominal region, the birds had large bare areas.

The beak was mostly grayish to purple but the proximal third of the lower mandible and much of the region of the commissural points was yellowish. The egg tooth persisted as a white spot near the tip of the upper mandible. Culmen length was about 20 mm and the width of the gape 18 mm.

At this stage the young were very alert and huddled together in the nest. They usually faced in different directions and the tip of each one's bill was slightly elevated to lie near the perimeter of the nest cup. Generally they no longer begged from a hand held above the nest and crouched deeply into the nest when we tried to remove them. Preening was observed at this time.

Days 21-22.—The tenth primary was about 38 mm long and the outer rectrix averaged 27 mm. Thus the remiges are more than one-half grown while the rectrices are less than one-third developed.

Dorsally the birds were almost fully feathered; the juvenal plumage was grayer and more drab than the brighter bluish hues of the adults. Although the sternal region was quite well-feathered, particularly anteriorly where feathers averaged 18–20 mm long (ad. = 35 mm), the young still showed bare spaces ventrally. The ventral feathers in general and the under tail coverts in particular were grayer than the dorsal feathers. The feathers of the femoral and crural regions were little developed.

The beak was still a yellowish-horn color basally and showed a tiny white remnant of the egg tooth. This was lost as the young bird began to use the bill in active food gathering. Culmen length had increased to about 21–22 mm while the reduction in amount of fleshy tissue at the jaw angle accounted for a slight reduction in width of gape to about 17 mm.

The tarsometatarsus had apparently almost stopped growing and was approximately adult size (42 mm). The toe span averaged about 49 mm and was almost as great as that of adults, although the claws still lengthened a bit after this time.

Weights of our captive birds at this age varied considerably depending upon whether or not they had recently been fed. As one bird easily consumed over 12 g of food within a few seconds, weight was not a very good indicator of age at this stage.

Birds typically fledged during this interval by parachuting out of the nest. They were poor fliers, could not maintain horizontal flight, and were fairly easy to catch once they were located. We found many recently fledged birds as they cowered in the grass and shrubbery or at the bases of larger trees. They sat quietly until discovered and then tried to escape by hopping and fluttering away. Most of these young would have escaped our notice had we not known that active nests were nearby. While chasing young birds we usually received a harsh scolding from a group of 5 to 12 adults that hovered nearby while we searched. We found a number of fledged young from different nests when we heard them beg from adults caring for them. If these young were frightened into leaving the security of their perches it was usually possible to run them down, as they flew only a few hundred feet at most before landing exhausted. Several birds captured after leaving previously undisturbed nests had measurements within the ranges given above.

4 weeks.—The major flight feathers were sheathed basally, primaries for approximately one-eighth their lengths, and rectrices for one-fifth their lengths. The upper wing coverts were fairly well-developed but the greater under primary and secondary coverts were pins from 5–15 mm long. Feathers of the anterior portion of the spinal tract were well-developed, but posteriorly they were considerably shorter than those of adults. Those of the midcoronal region averaged 11 mm (ad. = 13 mm), those of the cervical region were 27 mm (ad. = 27 mm), dorsal feathers averaged 30 mm (ad. = 48 mm), pelvic feathers were 19 mm (ad. = 42 mm), and the upper tail coverts were about 28 mm (ad. = 45 mm). The actual difference in amount of plumage was even greater than implied by these measurements, as feathers of adults had broader vanes and were stouter. The whitish tubercle representing the egg tooth was now gone in most birds.

At this age the young were still cared for by their parents and other birds although they did obtain some of their own food. On 20 May 1969 two banded young that had hatched on 20 April were seen actively foraging on the ground and probing into crevices of tree trunks. Young jays were capable of making flights of up to a few hundred feet, but they made no long sustained flights across broad expanses of open ground. They gathered in nursery groups consisting of the fledglings from several broods (Balda and Bateman, 1971). In spite of their rather large size, fledglings of this age had many features distinguishing them from adults. Most noticeably the tail was still stubby, the outer rectrices being equal to or only slightly longer than the outermost primaries. The plumage was primarily grayish rather than the richer blue of adults. The basal portion of the bill from the nostril caudad was a pale yellowish rather than black as in older birds. The darker distal portion of the bill was not so glossy black as that of adults. The bill was shorter and more blunt in young birds averaging 25–28 mm in culmen length as opposed to an adult average of 33.5 ($n = 10$). This measurement shows considerable sexual dimorphism, as Brodkorb (1936) pointed out. In our small sample culmen length of five males averaged 35.5 mm (33.9–37.4), that of five females was 31.5 mm (30.0–33.6). As the sexes of young in our study were not determined, we do not know when this dimorphism first becomes apparent.

6 weeks.—The remiges had virtually completed their growth. The average length of primary 10 in five young birds was 57.2 mm (54–60) while that of 15 adults was 59.0 (56–65). The tail feathers were still incompletely grown, the outermost averaging 88.8 mm (84–95) in five young and 101.7 (96–109) in 15 adults. Young of this age flew proficiently.

8 weeks and older.—Growth of the rectrices was just completed. The bluish-gray flight feathers were markedly brighter than the rest of the plumage. The inner vane of the remiges was more brownish than in adults. Rectrices were blue above and gray below. The postjuvenal molt was just beginning. New pins were evident along the edges of the humeral tract and interscapular region of the dorsal tract. The marginal coverts were being replaced proceeding posteriorly from the anterior edge of the propatagium. Blue feathers generally first appeared on the head in the occipital region and anteriorly at the angle of the jaw and frontal region.

Young observed in June, July, and August were typically undergoing the postjuvenal molt. By early August one captive 18-week-old Piñon Jay had a completely black bill. Four other birds, two 16-weeks- and two 18-weeks-old, still had a very small pink edging on the fleshy part of the gape.

FIRST FALL AND WINTER

After completing the postjuvenal molt young birds were still separable from adults in the field. Ventrally the young were grayer. The necklace of whitish feathers on the throat was not so distinct as in adults because the feathers of the malar and postauricular regions were a lighter blue. Dorsally the first-winter plumage was distinctive as it lacked the intensity of coloration seen in the adults, particularly on the head.

When specimens were examined closely the differences between adults and first-year birds were even more pronounced. Differences in color intensity were most apparent; young birds lacked the more brilliant bluish hues of adults. The flight feathers of the adults were more heavily built and proportionately broader, and the adults' outer primaries were slightly more truncate than those of young, but this difference was rather subtle. Additionally, as Pitelka (1945) noted for *Aphelocoma,* the tips of the rectrices of older birds were more truncate. Those of young appeared to show greater signs of wear than those of adults collected at the same time, reflecting the greater age and more frail nature of the juvenal rectrices. In *Gymnorhinus* the shape of the tail as a whole is not distinctly different in young from that of adults. The tail of the Piñon Jay is markedly shorter than that of many other jays and the rectrices are not noticeably graduated.

Retained juvenal greater primary and secondary coverts were distinctly duller in coloration than coverts that were replaced during the molt, these latter being bluer than the grayish-brown juvenal coverts. In birds collected while in the first-winter plumage the difference in coloration of juvenal and replaced coverts easily allowed them to be identified as young born the previous nesting season.

TABLE 3
MEAN WEIGHTS OF YOUNG OF *GYMNORHINUS CYANOCEPHALUS* IN GRAMS

Age in days	N	x̄ ± SE	Range	Age in days	N	x̄ ± SE	Range
0	26	6.26 ± 0.208	4.0– 8.6	9	11	46.46 ± 3.189	28.0–60.5
1	16	8.07 ± 0.238	5.3– 9.4	10	8	55.56 ± 3.491	43.0–70.0
2	29	11.70 ± 0.473	6.4–17.3	11	8	62.33 ± 3.886	48.3–77.5
3	9	14.33 ± 1.760	10.7–28.0	12	8	62.60 ± 3.064	54.1–78.2
4	23	22.55 ± 1.480	13.5–36.0	13	8	64.08 ± 2.719	51.9–77.8
5	9	24.83 ± 0.878	20.5–29.4	14	10	73.54 ± 3.519	55.4–88.4
6	17	33.81 ± 1.420	24.8–41.7	17 (15–19)	21	75.79 ± 1.589	64.1–90.6
7	12	40.28 ± 0.562	36.6–42.2	22 (20–24)	7	78.89 ± 1.622	73.5–84.5
8	9	43.73 ± 2.473	26.7–50.5	26.5 (25–28)	5	81.30 ± 4.470	71.8–96.3

GROWTH

As Piñon Jays typically are early nesters (but see Ligon, 1971) they contend with a number of factors that seemingly might impair nesting success. Perrins (1970) has shown that for some species there is strong selection pressure to breed early in the year. He suggests that the food supply available to breeding females immediately prior to the breeding season is the main factor influencing their ability to form eggs, and females not finding sufficient food are forced to lay later and raise their young at a time when food to nourish them is less readily available.

Piñon Jays nesting in late February and early March in the Flagstaff area (7,000 feet) seemingly breed at a disadvantageous time. Insects are generally less active and often covered by snow. Courting males feed females large amounts of food, which is probably important in supplying some of the energy needed for forming eggs (Lack, 1966; Perrins, 1970). Cold temperatures (Table 1) force the female to brood the young almost continuously for part of the nestling period, and the male feeds both the young and the female. This situation produces some of the same disadvantages faced by those species whose young are cared for by a single parent (Lack, 1968). When young are well-feathered and ambient temperatures favorable both parents seek food. These circumstances generally occur during the latter part of the nestling period and allow greater amounts of food to be brought to the nest when energy requirements of the brood are presumably highest. Selection would seem to favor a rapid growth rate leading to a greater heat conserving ability. In contrast, great lability in growth rates would be selectively advantageous owing to high variation in food availability from year to year. The fact that a number of broods contained one or two young that were younger than most of their siblings suggests that food is a factor limiting

TABLE 4
LENGTH OF OUTER PRIMARY OF *GYMNORHINUS CYANOCEPHALUS* IN MILLIMETERS

Age in days	N	x̄ ± SE	Range	Age in days	N	x̄ ± SE	Range
0	—	—	—	16	4	24.38 ± 0.987	21.5–26.0
1	—	—	—	17	7	28.71 ± 1.742	22.0–36.0
2	—	—	—	18	3	30.50 ± 1.041	18.5–32.0
3	—	—	—	19	2	33.00 ± 1.500	31.5–34.5
4	7	1.00 ± 0.000	1.0	20.5 (20–21)	3	37.00 ± 1.732	34.0–40.0
5	4	1.88 ± 1.048	1.0	22.5 (22–23)	3	39.67 ± 1.167	37.5–41.5
6	9	1.50 ± 0.250	0.5– 5.0	24.5 (24–25)	3	43.67 ± 1.764	41.0–47.0
7	8	3.07 ± 0.170	2.5– 4.0	26.5 (26–27)	3	46.67 ± 2.028	43.0–50.0
8	4	3.75 ± 0.250	3.0– 4.0	28.5 (28–29)	3	49.33 ± 2.028	46.0–53.0
9	12	5.83 ± 0.534	2.0– 8.0	32 (30–34)	6	51.75 ± 1.471	47.5–57.0
10	10	8.75 ± 0.775	5.5–12.0	37 (35–39)	5	54.80 ± 1.513	50.0–58.5
11	8	11.63 ± 1.824	5.0–19.0	42 (40–44)	4	57.13 ± 1.533	54.0–60.0
12	8	16.38 ± 1.319	9.5–20.0	47 (45–49)	4	57.13 ± 1.533	54.0–60.0
13	8	18.06 ± 0.710	16.0–22.5	52 (50–54)	4	58.00 ± 1.500	55.0–59.5
14	10	24.85 ± 0.949	19.0–28.0	57.5 (55–60)	4	59.75 ± 0.250	59.5–60.0
15	2	25.50 ± 2.500	23.0–28.0				

nesting success (Lack, 1954, 1966, 1968). Data on growth were obtained from 89 young of known age from 25 nests (Tables 3, 4, and 5).

Increase in weight.—On day 0, 26 hatchlings had an average weight of 6.26 g (Table 3), which is 95 percent of the average weight of an egg (x̄ = 6.65, n = 199). Holcomb and Twiest (1968) reported that

TABLE 5
LENGTH OF OUTER RECTRIX OF *GYMNORHINUS CYANOCEPHALUS* IN MILLIMETERS

Age in days	N	x̄ ± SE	Range	Age in days	N	x̄ ± SE	Range
0	—	—	—	16	4	10.38 ± 0.657	9.0–11.5
1	—	—	—	17	7	16.86 ± 1.818	13.0–25.0
2	—	—	—	18	3	16.33 ± 0.726	15.0–17.5
3	—	—	—	19	2	19.00 ± 2.000	17.0–21.0
4	—	—	—	20.5 (20–21)	3	24.00 ± 2.021	21.5–28.0
5	5	0.20 ± 0.200	0.0– 1.0	22.5 (22–23)	3	31.50 ± 2.180	28.0–35.5
6	9	0.89 ± 0.111	0.0– 1.0	24.5 (24–25)	3	37.50 ± 2.930	33.0–43.0
7	8	0.75 ± 0.094	0.5– 1.0	26.5 (26–27)	3	43.17 ± 2.728	39.5–48.5
8	4	0.86 ± 0.125	0.5– 1.0	28.5 (28–29)	3	49.00 ± 2.843	45.0–54.5
9	12	1.95 ± 0.265	0.5– 3.5	32 (30–34)	6	55.83 ± 2.565	49.5–66.0
10	10	2.20 ± 0.351	1.0– 4.0	37 (35–39)	5	66.80 ± 4.451	57.0–81.5
11	8	5.75 ± 0.945	2.5–10.0	42 (40–44)	4	77.38 ± 3.613	69.0–85.0
12	8	6.38 ± 0.844	2.0– 8.0	47 (45–49)	4	85.50 ± 2.843	79.0–92.0
13	8	6.88 ± 0.817	4.0–12.0	52 (50–54)	4	89.50 ± 2.170	85.5–93.5
14	10	11.85 ± 1.008	6.5–15.5	57.5 (55–60)	4	89.50 ± 2.021	86.0–93.0
15	2	13.00 ± 4.000	9.0–17.0				

TABLE 6
CHANGES IN BODY WEIGHT AND IN LENGTH OF OUTER PRIMARY AND OUTER RECTRIX WITH AGE

	Age			
	0 days	10 days	Fledging	Maturity
Increase in weight				
Number	26	8	2	14
Mean weight (g)	6.26	55.56	78.00	103.30
Multiple of weight at day 0	1.00	9.17	12.99	17.17
Percent adult weight	6.06	53.79	75.51	100.00
Absolute increase (g)	0	49.30	22.44	25.30
Growth of outer primary				
Number	26	10	3	15
Outer primary (mm)	0	8.75	37.00	59.00
Percent adult length	0	14.83	62.71	100.00
Absolute increase (mm)	0	8.75	28.25	22.00
Growth of outer rectrix				
Number	26	10	3	15
Outer rectrix (mm)	0	2.20	24.00	101.70
Percent adult length	0	2.16	23.60	100.00
Absolute increase (mm)	0	2.20	21.80	77.70

neonate Red-winged Blackbirds (*Agelaius phoeniceus*) were 79 percent of the weight of fresh eggs. Wetherbee and Wetherbee (1961) reported a similar figure (73 percent) for both the Brown-headed Cowbird (*Molothrus ater*) and Common Grackle (*Quiscalus quiscula*). The rather large discrepancy between previously published figures and those reported here are no doubt partly caused by the fact that most hatchlings in our study were first weighed in the afternoon, but hatched in the morning and may have been fed before being weighed. One young bird hatched sometime after 17:07 on 16 April weighed only 4.0 g the following morning at 10:30. The egg from which it hatched weighed 6.6 g on date of laying. Thus the hatchling was only 60.6 percent of the weight of the fresh egg. Two young weighed at 12:40 averaged 5.25 g (5.1, 5.4) after having been fed at least once. Four other young weighed by 11:00 on the day of their hatching averaged 5.7 g (5.4–6.1), which was 86 percent of average weight of eggs. These young had probably been fed at least once prior to weighing.

Nestlings gained weight rapidly and were fed mostly insects (*contra* Turček and Kelso, 1968), particularly orthopterans. During the early nestling period adult males gathered most of the food for the females and brood. As young grew, became endothermic, and needed more food, the females also became active foragers, particularly during warmer hours of the day. This activity by females was curtailed during colder weather.

At the age of 10 days the young Piñon Jays had attained 53.8 percent of the adult weight (Table 6). Holcomb and Twiest (1968) reported a like figure for male Red-winged Blackbirds (54 percent) and felt that these birds were perhaps somewhat slow in their development, at least as compared to other passerines, as Nice (1943) reported that young of several passerine species reached 60 to 80 percent of adult weight by 10 days.

During the second half of their nestling period (days 11–21) Piñon Jays have a greatly decreased weight gain. The absolute weight gain during the latter half of the nestling period was only about 50 percent of that experienced in the first half, but feather growth was most pronounced during the second half (Table 6). A number of authors (Kendeigh and Baldwin, 1928; Banks, 1959) have suggested that the decrease in rate of weight gain that often occurs in the latter half of the nestling period is related to increased energy demands for feather growth and temperature regulation. The metabolic drain associated with feather and heat production might be expected to necessitate compensatory adjustments, particularly in those organisms operating within a limited energy budget.

Ricklefs (1967b) presented a graphical method of fitting equations to growth (as shown by increase in weight) curves. The following logistic equation most accurately portrays the growth of the Piñon Jay:

$$W = \frac{A}{1 + e^{-K(t_w - t_0)}}$$

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_0 is the age in days at the point of inflection on the growth curve. Using appropriate procedures (Ricklefs, 1967b) we determined that K for the Piñon Jay is 0.328. The equation describing the growth of the Piñon Jay is:

$$W = \frac{78.9}{1 + e^{-0.328(t_w - 7.6)}}$$

The age at the point of inflection of this curve is 7.6 days as determined from the converted growth curve and represents the age at which nestling growth, as defined by the asymptote of weight approached by nestlings (78.9 g in this case) is one-half completed.

The value of K of various species whose growth is described by the logistic equation is an expression of how fast an animal completes nestling development, but it does not make growth rates directly comparable as related to actual increments of weight added. Thus the Cactus Wren

(*Campylorhynchus brunneicapillus*), which has a K value of 0.394 (Ricklefs, 1967b), grows 1.20 (0.394/0.328) times as fast as the Piñon Jay according to a comparison based upon time necessary to complete nestling growth. Yet relative to the Cactus Wren, which increased its weight at day 0 by a multiple of 7.9 by day 10, and gained 23.5 g in the process, the Piñon Jay showed a more rapid increase in relative and absolute size. Its weight increased by a multiple of 9.2 and it gained 49.3 g during the same interval (Table 6). The Snow Bunting (*Plectrophenax nivalis*), K = 0.552 (Ricklefs, 1967b) grows 1.68 (0.552/0.328) times as fast as the Piñon Jay. The slower rate of growth seen in the Piñon Jay is not unexpected as it has previously been noted (Ricklefs, 1968a) that growth rates are inversely correlated with body size.

Values for the overall growth rate index (K) given by Ricklefs (1968a) for other corvids are: K = 0.172 for *Corvus brachyrhynchos* from Illinois (asymptote of nestling weight = 450 g); K = 0.332 for *Pica pica* from Germany (asymptote = 190 g). Comparison of observed and expected time intervals for each of these species to grow from 10 percent to 90 percent of asymptotic weights indicates that the crow grows more slowly than expected based upon its body size (observed = 25.5 days, expected = 21.5 days) while the magpie grows more rapidly than expected (observed = 13.3 days, expected = 17.7 days).

Based upon Ricklefs' (1968a) regression equation for correlation of growth rate and body size, the Piñon Jay has an expected time interval of 13.3 days to grow from 10 percent to 90 percent of asymptotic weight approached by nestlings. The observed value for this interval based upon our data is 13.4 days.

The relationship between the weight attained at the end of the nestling growth period and adult weight seems logically to be generally descriptive of the state of development of the young at fledging. In our captive jays increase in weight seemed relatively smooth until about 27 days of age (approximately 6 days beyond normal fledging age). At this time the young, both in the wild and captivity, were not fed so frequently and were learning to feed themselves. Consequently weights of individuals were highly variable. The ratio (R) between their weight at this age (81.3 g, n = 5) and that of adults (103.3 g, n = 14, 7♂♂, 7♀♀) is 0.787. Ricklefs (1968a) found that only 14 of 55 passerine species for which this ratio was determined had such a low value (or were so relatively undeveloped). He determined that this ratio seemed most highly correlated with the way adults foraged. Values of R less than 0.9 appeared most commonly in ground feeding species. Presumably some of the differences in fledgling/adult ratios are related to the degree of per-

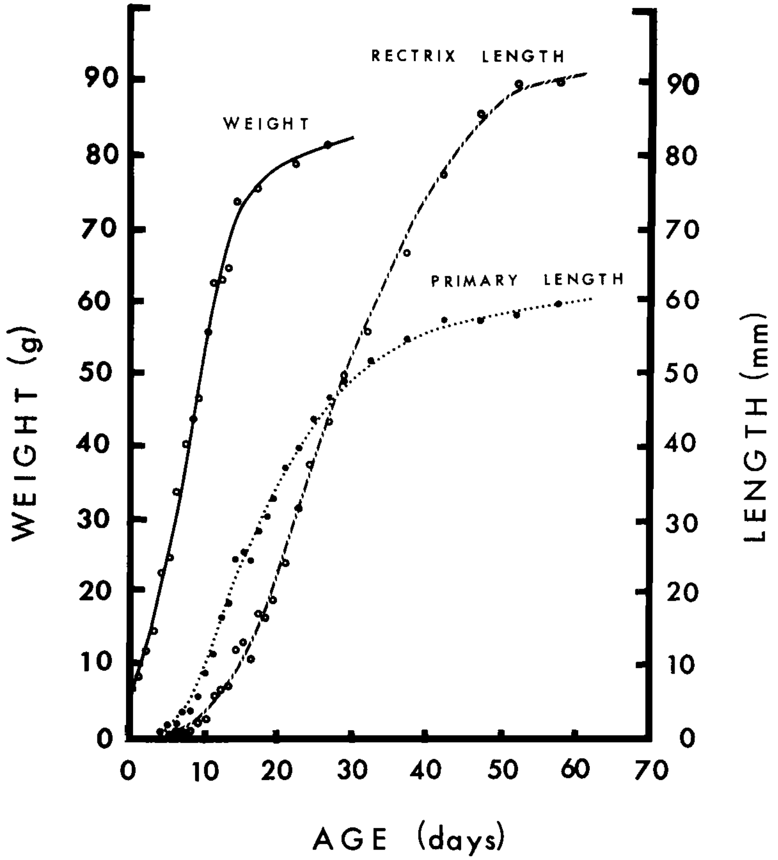

Figure 1. Changes in body weight and lengths of the outer primary and the outer rectrix of young Piñon Jays.

fection of the structures (i.e. muscles, bones, and feathers) comprising the flight apparatus (Ricklefs, 1968a). It is mentioned above and elsewhere (Balda and Bateman, 1971) that fledgling Piñon Jays are extremely weak fliers. These birds support Ricklefs' (1968a) hypothesis that ground feeders do not have to be so well-developed at fledging as do aerial or arboreal feeders. The hind limbs have reached adult proportions at fledging, indicating a strong dependence on these structures. The system of communal care and feeding of young that exists in this species does not require the young to have great flight proficiency.

Feather growth.—Growth of flight feathers (remiges and rectrices) rather closely followed that of general body plumage. Primaries initiated rapid growth sooner than did the rectrices (Figure 1). Although short brushes sometimes appeared by 4 days, the rectrices did not start active growth until day 8 or 9. The fact that feather growth does not commence sooner after hatching suggests that increase in body size, and thus in volume to surface ratios, may surpass the value of an insulative cover during early nestling life. Part of the selective advantage of larger size is probably related to increased efficiency of functions other than thermoregulation (i.e. digestion, coordination of begging behavior, etc.).

Primaries held a significant edge in length until about 4 weeks of age, when primary growth began to level off (Figure 1), although the tail continued its rapid growth. Young of this age were becoming capable of longer flights. Certainly the increased surface area provided by the rapidly growing flight feathers would have lessened wing loading to a considerable degree. As the tail at this point was still somewhat less than half adult size, its value as a steering and braking organ was limited, but flights undertaken at this time normally did not require a high degree of maneuverability.

Food and Feeding Rates

Most food for nestlings was gathered by adult males, who foraged together in small flocks in open parts of the ponderosa pine forest. Plants showed few signs of active growth at this season (March to mid-May) and ground cover consisted of the dried remains of *Amaranthus, Bouteloua, Cleome, Helianthus,* and *Salsola.* Scattered clumps of *Chrysothamnus* and *Gutierrezia* were also present.

Groups of 6–8 males usually returned to the nesting area more or less synchronously. Males fed their mates and young by regurgitation. This involved strong lateral shaking motions of the head usually followed by extension of the neck. Food samples removed immediately from the throats of nestlings were covered with copious amounts of a clear, mucilaginous secretion.

As few as 3 food samples were collected from one nest and as many as 34 were gathered over a 15-day period from another; in all 80 samples were obtained from the young of 6 different broods.

Contents of each sample were identified to family for insects, ordinal levels for other arthropods, and species for seeds and vertebrate remains. Bits of eggshell found in one young and gravel found in nine young were excluded from the analysis. Also excluded were the very few food items not identifiable to the desired level; these included: a bit of plant root, a leaf fragment, one hemipteran, one coleopteran, and two other partly digested insects. The plant matter and gravel may have been fed the young accidentally although Ligon (1971) recorded nestlings being given gravel with some regularity. Gravel may be helpful in grinding

TABLE 7

FOOD OF NESTLING PIÑON JAYS BASED UPON 80 SAMPLES CONTAINING 512 ITEMS

Taxon	Frequency[1]	Numerical percent composition[2]
Spermatophyta		
Gymnospermae		
Pinus edulis seeds[3]	38.75	8.77
P. ponderosa seeds	1.25	0.39
Angiospermae		
Oat seeds (*Avena* sp.)	3.75	2.15
Arthropoda		
Arachnida		
Araneae[3]	46.25	15.82
Insecta		
Orthoptera		
Gryllidae[3, 4]	60.00	16.41
Acrididae[3, 4]	47.50	20.51
Phasmidae	1.25	0.20
Hemiptera[4]		
Miridae	2.50	0.39
Reduviidae	1.25	0.20
Lygaeidae	2.50	0.39
Scutelleridae	3.75	0.59
Pentatomidae	2.50	0.39
Homoptera		
Cercopidae	2.50	0.39
Neuroptera		
Myrmeleontidae[5]	2.50	0.59
Coleoptera		
Carabidae[3]	23.73	7.03
Staphylinidae	1.25	0.20
Dermestidae[5]	1.25	0.20
Buprestidae	2.50	0.39
Tenebrionidae	1.25	0.20
Scarabaeidae	16.25	2.34
Chrysomelidae	1.25	0.20
Curculionidae	7.50	1.37
Lepidoptera[5]		
Pieridae	1.25	0.20
Arctiidae	10.00	4.88
Noctuidae[3]	27.50	5.66
Lasiocampidae	11.25	3.91
Geometridae	1.25	0.20
Tineidae	2.50	0.39
Diptera[5]		
Otitidae	1.25	0.20
Tephritidae	12.50	3.91
Oestridae	1.25	0.20
Hymenoptera		
Ichneumonidae	1.25	0.20
Vespidae	1.25	0.20
Megachilidae	3.75	0.59
Chordata		
Squamata		
Sceloporus undulatus	3.75	0.59

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[1] Percent of samples in which this food class occurred.

[2] Percent of all items found belonging to this class.

[3] Numerically these six taxa account for about three-fourths of food items collected from young jays.

[4] Mostly nymphs.

[5] Larvae.

up insect food, but dissection of nestling jays showed that even those with no gravel in the digestive tract had successfully ground their insect food into tiny fragments. Possibly the harder portions of the insect exoskeletons aid in trituration.

Nestling birds were collared as early as 09:45 until as late as 17:35. No correlations were noted between time of day and nature of food supplied to young. It would be interesting to monitor food brought much earlier in the day when insects are less active, for they might constitute less of the diet and be replaced by more readily available food, such as seeds. We considered it unwise to disturb nests earlier in the day, as females usually brooded young at this time, particularly on cooler mornings.

In order to assess the relative importance of various classes of food in the diet we computed two parameters, the frequency of occurrence and percent contribution to the total diet based on numerical density (not weight) of each taxon to the total of all samples (Table 7). The top six classes of food, in terms of occurrence and percent composition comprised about three-fourths of the diet. They varied in frequency of occurrence from 23.73 to 60.00 percent.

The relative importance of terrestrial foraging is obvious from the food samples. Five of the six most important classes of food are essentially restricted to ground and herbaceous strata during the spring months. These include acridid grasshoppers, gryllids, piñon seeds, carabids, and larval noctuids. The other important food type, spiders, although occurring in arboreal situations, are apparently most abundant in lower strata (Balda, MS). The piñon pine seeds fed to the young are those harvested earlier from trees on nearby cinder cones and cached in the vicinity of the nesting grounds (Balda and Bateman, 1971).

The only vertebrate remains encountered in the food samples were those of an adult (ca. 70 mm snout-vent length) *Sceloporus undulatus*. The lizard had been sectioned into roughly thirds and fed to nestlings 4 days old. Judging from its freshness, the lizard was not taken as carrion. Ligon (1971) also reported a lizard of this species fed to young Piñon Jays in New Mexico. Once in early spring we saw two adult Piñon Jays attack and kill a lethargic short-horned lizard (*Phrynosoma douglassi*). Upon recovering the lizard we noticed it had several lacerations and punctures about the head region; mostly around the eyes. The lizard was an adult and measured over 80 mm in snout-vent length. A similar method of killing or incapacitating food objects was noted with large lepidopterous larvae. Almost without exception these showed evidence of having been struck on the head, and a number had the entire head capsule removed. The distal segments of the hind limbs of most of the acridids had been removed as reported by Ligon (1971). Other food items such as ground crickets (*Nemobius fasciatus*) showed no signs of any special treatment before being fed to the young. A conspicuous feature of the nestling diet is its tremendous diversity. In our samples we were able to identify 35 major taxa, only 4 of which were not arthropods. Owing to the low temperatures and periodic snowfall that prevailed while we collected food samples in 1970, arthropods were extremely inconspicuous. The wide range of species in our samples is a tribute to the foraging diversity and efficiency of the parent jays.

Regarding changes in feeding rates through the course of the nestling period our data are merely suggestive. The number of feeding visits by parents seemed very low. In over 60 hours of observation at nests where young and parents were unmolested and where observation periods lasted at least a full hour, the visits averaged 1.52 per 100 minutes. There seemed to be a slight increase in number of trips as the nestling period advanced. During its first half (days 0–10) parents averaged one trip per 74 minutes, during the latter half (days 11–21) they averaged one trip per 58 minutes of observation time. It is important to remember that the male often fed his mate during the early half of the nestling period, whereas later the female fed herself as well as the young.

We have some limited information on the actual amounts of food parents brought to the nest. Nestlings of one brood of four were fed at the rate of 3.4 items per bird per hour when watched over a 5-hour period on the 4th day after hatching. The three surviving nestlings when watched over a comparable 5-hour period on their 12th day received an average of 6.3 items per bird per hour. At least some of this increase is attributable to the fact that this particular brood suffered a reduction in numbers; hence, the feeding rate would increase with no change in parental activity. The absolute number of visits accounting for these food items is unknown as the nest was not watched continuously. We have no direct information regarding the amounts of food adults carried per feeding visit, but from the numbers of items found in the throats of young, the number of young per nest, and observed rates of nest visitation, we calculate that feeding birds were bringing from 16.2 to 18.6 items per visit. The lower figure is almost certainly too low, as some of the food brought early in the nestling period was given to the adult females and thus not considered in our calculations. Although these figures for items being carried are quite high, we feel that they are easily within the birds' capabilities. We have collected adult birds with as many as 27 intact piñon pine seeds in the throat.

To calculate the number of young fed per visit, we summed the total number of sampling intervals in which at least one young was fed (thus at least one feeding visit had occurred) and determined the potential number of individual feedings. From our data about 70 percent of such potential feedings were realized. Thus, in our average brood of 3.4 (n = 6) an average of 2.4 young were fed during a single feeding visit. Sometimes a parent fed all the young on a single visit, as Ligon (1971) also reported.

DISCUSSION

Our data suggest that growth and development of nestling Piñon Jays are fairly typical for a passerine species of its size. This is somewhat surprising considering the rigorous nesting environment. Some features of the developmental process, however, deserve comment.

The nestling's skin becomes very dark by about the 7th day, and before any pronounced feather growth starts. The young then weigh about 40 g each; this figure is about at the inflection point of the weight-gain curve. Because of increased energy demands for maintenance as well as accelerated feather growth, it is advantageous for the female to brood less and forage more for the young during warmer periods of the day. The dark skin and the fact that most nests are placed on the south side of the tree (Balda and Bateman, 1972) aid in absorption of solar radiation. This helps conserve energy needed for maintenance.

The nestling jay diet consisted of about 89 percent animal matter and 11 percent vegetable matter based on numerical composition. Piñon pine seeds formed a regular portion of the diet, being present in almost 40 percent of the samples. Piñon pine seeds contain the following proportions of the three basic food elements: protein 14.5 percent, fat 60.1 percent, carbohydrate 18.7 percent (Botkin and Shires, 1948). The high proportion of fats and carbohydrates in this food source is important, not only in supplying energy for maintenance, but may also serve in the buildup of fat reserves. Stored fat could be important to young facing the threat of starvation and might also serve an insulative function. This latter would be especially important on cold nights, which are common in our study area.

Although not unique to this species, the more rapid development of the dorsal plumage was especially striking. Young were fully covered dorsally by 15 days of age, but not ventrally until after leaving the nest. Thus, heat loss was probably greatly reduced by the extensive plumage above and the nest lining below.

As Ricklefs (1969) pointed out, the capabilities of the parents in caring for the young may be of greater significance to nesting success than any specific adaptations of the young. In the Piñon Jay not only is the role of the parent in providing food and caring for the young of importance, but certain aspects of sociality such as communal care of the young and increased protection afforded by the flocking behavior (Balda and Bateman, 1971) also help insure nestling success.

Feeding rates of most passerine nestlings are higher than those of the Piñon Jay, which averaged about one feeding trip per 66 minutes of observation. Yet the Piñon Jay, for its size, grows as rapidly as most other passerines. Though the frequency of feeding visits appears low, it is almost identical to the rate Mewaldt (1948) reported for another early nesting corvid, Clark's Nutcracker. Brown (1970) considered the rate of feeding trips by the Mexican Jay (*Aphelocoma ultramarina*) to be low; over 110 hours of observation it averaged 7.05 visits per 100 minutes, or more than 4½ times the figure for the Piñon Jay. Brown (1970) gave no information on the nature or amounts of food given young Mexican Jays nor on the average number of young fed per visit. Although he counted only feeding visits, the incentive of helpers to provide food for young Mexican Jays was perhaps not so great as that of the actual parents in the Piñon Jays. Some visits in the former species may have had a primarily social rather than nutritive function.

Parental care of the nestling Piñon Jay seems no less efficient than the system of communal feeding in the Mexican Jay. Young Piñon Jays leave the nest at 21 days, whereas the similar-sized Mexican Jay does not fledge until 25 days. Although habitats occupied by the two species may not be equally rigorous in their demands upon nesting birds, morphological and behavioral adaptations of the Piñon Jay that allow large amounts of food to be carried at each visit are highly efficient in terms of conservation of the parents' energy. Similar adaptations are known for Clark's Nutcracker (Bock, Balda, and Vander Wall, MS) and probably explain the protracted intervals between feeding trips Mewaldt (1948) noted in that species.

Ricklefs (1968a) noted that the state of development of the young at fledging is related to the degree of perfection of the flight apparatus and is correlated with the foraging pattern of adults. As shown earlier, Piñon Jays leave the nest in a relatively undeveloped condition. The advantages to this species of fledging while in this state are probably related to two factors: greater opportunity for obtaining food and increased protection by flock members. Nestling Piñon Jays are cared for solely by the parents until near the end of the nestling period when other members of the flock may visit the nest (Balda and Bateman, 1971). As soon as the young leave the nest they may beg vigorously from any member(s) of the flock. Begging was the most conspicuous and frequent behavior pattern we observed in these young birds. We have seen young begging vociferously from their parents, other adult Piñon Jays, fledgling and yearling Piñon Jays, and on two or three occasions from Robins (*Turdus migratorius*) and Clark's Nutcrackers. As there may be in the general vicinity of fledged young many adult and yearling birds that are not caring for nestlings, the recruitment of such individuals to care for the young may contribute to the overall productivity of the flock. Seemingly the most vigorous and consequently most conspicuous young are fed most often, and thus favored within the communal situation by natural selection.

By acquiring status as new flock members the young jays gain an increased measure of protection from predators. It might seem that by joining a flock young birds expose themselves to increased predation because of the assembled group's conspicuousness, but even isolated individuals would be apt to attract predators as they beg very loudly. We have seen flock members successfully drive away various types of predators on a number of occasions and have evidence that the intensity of mobbing behavior is directly related to the number of birds present. Thus by being part of a larger group the young jays receive more protection, and potentially more food, than they might if they remained more or less isolated.

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SUMMARY

Growth, development, and food habits of young Piñon Jays were analyzed from data gathered over a 3-year period. Eggs require 17 days of heat application to hatch. Hatching, at least of larger clutches (4–5 eggs), is often asynchronous because females tend to initiate incubation with the penultimate or antepenultimate oviposition. Staggered hatching of eggs within a single clutch suggests that food for nestlings is a critical factor limiting nesting success.

Growth data were obtained from 25 nests containing 89 young of known age. At 10 days of age young Piñon Jays averaged 9.2 times as heavy as on the day of hatching. During the latter half of the nestling period (days 11–21) increase in weight was greatly reduced while plumage

growth was pronounced. Nestlings were fed a diet comprised mostly of insects, although piñon pine seeds occurred in food samples regularly. Adults obtained most food items by terrestrial foraging and seemed extremely opportunistic in food selection. Frequency of feeding trips seemed low (one trip/66 minutes), but number of items brought per trip was high (15–20 items/trip). Comparisons with growth information available for other passerines show that the Piñon Jay grows about as fast as expected for a bird of its size. It fledges while still relatively undeveloped.

Several features allow the Piñon Jay to nest during periods of relative climatic adversity. The dark skin of the young and placement of most nests on southerly exposures aid absorption of solar radiation. Dorsal plumage tends to develop more rapidly than the ventral plumage. The plumage above and nest lining below afford significant insulative protection.

Perhaps efficiency of the adult Piñon Jays is more important to nestling success than are any specific adaptations of the young. The adults' opportunistic collection of food and ability to carry large amounts on each feeding trip increase the young birds' chances of survival.

After fledging certain aspects of sociality such as communal care of the young and increased protection from predators afforded by flocking are important in furthering their survival.

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