

MOLT AND ITS TIMING IN THE PIÑON JAY, *GYMNORHINUS CYANOCEPHALUS*

J. DAVID LIGON AND JAMES L. WHITE¹

Department of Biology
The University of New Mexico
Albuquerque, New Mexico 87131

Piñon Jays (*Gymnorhinus cyanocephalus*) exhibit several traits which make them of special interest and which in combination serve to set them apart from other North American members of the family Corvidae: (1) they may wander widely and are often characterized as nomadic; (2) they often nest colonially (Balda and Bateman 1971); (3) they may breed very early, e.g., February (Jensen 1923; Ligon 1971); (4) populations in southwestern New Mexico breed in late summer and early autumn in some years (Bailey 1928; Ligon 1971); and (5) the annual molt is interrupted during this late breeding (Ligon 1971). All of these traits, plus others, are related to the species' use of seeds of piñon pines (*Pinus edulis*, *P. monophylla*) or, to a lesser extent, seeds of other conifers, e.g., ponderosa pine (*P. ponderosa*) (Balda and Bateman 1971). Seed production in the piñon pine is erratic both in time and space. The great reliance on this unpredictable food source has produced concomitant variation in the annual cycle of the Piñon Jay. This appears to be true particularly in southwestern New Mexico, the only portion of the species' range from which autumnal breeding has been recorded. One of our goals in this report is to relate molt in Piñon Jays of this region to other features of the annual cycle.

MATERIALS AND METHODS

Specimens used in this study were taken from two large flocks over a 4-year period, 1969–72. Most (232) were collected from a flock located 12 miles W of Magdalena, Socorro County, New Mexico. Ligon (1971) reported late summer-autumnal breeding and suspended molt in this population. The remaining jays studied (71) were taken from a flock 15 miles E of El Morro National Monument, Valencia County, New Mexico. This area is similar to that described by Balda and Bateman (1971, 1973) in that ponderosa pine is an important plant community. The area is higher and wetter than the Magdalena site. Specimens were collected systematically at about 2-week intervals for 1 year, August 1969–August 1970, from the Magdalena flock. Most taken in 1971 and 1972 were molting. Piñon Jays were collected May–August 1969 from the El Morro flock, and in

July in 1970 and 1971. Data on molt were obtained from 228 or 75% of the specimens collected. Most were preserved as flat skins for study of molt. In addition, age, sex, standard measurements, weight, stomach contents, and gonadal condition were recorded. In this paper we present gonadal conditions of adult males only as they relate to molt.

Captive Piñon Jays appear to molt normally in every way. Twenty adult males caged outdoors in groups of five were laparotomized at monthly intervals from 1 October 1971 to 1 September 1972. Ten of these were from the Magdalena flock and ten were from the Sandia Mountains near Albuquerque, New Mexico. Some members of the former flock bred in autumn 1969 (Ligon 1971), whereas there is no evidence that birds from the Sandia Mountains or the El Morro area ever engage in autumnal breeding.

Pterylography was studied by use of clipped preserved and fresh adult specimens. Feathers from the alar and caudal regions were removed singly from fresh specimens and mounted in a manner like that of Pitelka (1945:fig. 38) and Selander (1958:fig. 1). Pterylography of the Piñon Jay is similar to that of *Aphelocoma* jays and Clark's Nutcracker (*Nucifraga columbiana*) and the reader is referred to Pitelka (1945) and Mewaldt (1958) for illustration of the major feather tracts.

Molt in adults and yearlings begins with the first primary and is virtually complete with replacement of the sixth secondary. Slight molt, especially of the spinal tract, may continue beyond replacement of the sixth secondary. Thus, we have modified the molt scoring system used by many authors which utilizes only the primaries (e.g., Miller 1961; Newton 1966). Our system is based on the 10 primaries plus secondaries 5 and 6. With this minor change, a simple numerical system like that of Newton (1966) was employed to record molt. Each primary of each wing, plus secondaries 5 and 6, was scored 0–5 (not dropped—completely regrown). An overall value of "0" indicates that molt had not begun, whereas a score of "120" indicates that molt of the remiges was complete. The value "120+" indicates body molt that continued after complete replacement of the remiges. Molt stages 1–12 were based on the score obtained for the primaries plus secondaries 5 and 6; e.g., Stage 1 includes scores 1–10, Stage 2 includes scores 11–20, etc. Stages of wing molt are standards to which other aspects of the molt are compared.

Secondaries and rectrices were scored in a similar manner, making possible a quantitative description of the relationship between primary molt and molt of these feather groups. For plotting molt of secondaries and rectrices against primary molt, secondaries 5 and 6 were not included with the primaries.

Numerical values were not assigned to body molt. Rather, the feather tracts in which molt was occurring are indicated directly for each of the molt stages.

¹ Present address: 2430 Alvarado Drive, Albuquerque, New Mexico 87110.

Rates of molt were investigated in two ways: by means of regression analysis of wing molt score on date (see Evans 1966; Newton 1966; Niles 1972 for discussion of the use of linear regression in studies of molt); and by calculating the rate of increase in molt score per day in captives, e.g., a score of 10 on day 1 and a score of 55 on day 30 indicate an average rate of 1.5 points per day.

PTERYLOGRAPHY

Alar tract. There are 21 remiges: 10 primaries and 11 fully developed secondaries. "Tertials" are not distinguished from other secondaries. The outermost or 10th primary is well developed, although it is only about 40% the length of the longest primary, number 7. The presence of an 11th (innermost) secondary is surprising, as Pitelka (1945:234) states that "twenty remiges [10 primaries, 10 secondaries] are a common and probably characteristic number among corvids" (brackets ours). We found 10 secondaries in *Aphelocoma coerulescens*, *Nucifraga columbiana*, and *Corvus brachyrhynchos*. The eleventh secondary in *Gymnorhinus* is about half the length of secondaries 1-7.

There are 10 greater upper primary coverts; the 10th is greatly reduced. Distal to the bases of greater upper primary coverts 2-10 are middle upper primary coverts. Lesser upper primary coverts were not discernible. Following the terminology of Mewaldt (1958), the carpal remex is attached at the base of the first primary; the small covert distal to the first greater secondary covert is either the carpal covert (Mewaldt 1958) or, as suggested by Pitelka (1945:232), is the 10th (first) middle upper secondary covert. There is a small covert between the carpal covert and the base of the alula. In addition, the alula supports several small coverts at its base which probably are derived from the adjacent marginal coverts. The 11 greater upper secondary coverts are attached at the base of, and proximal to, each corresponding secondary. There are nine middle upper secondary coverts which alternate with the greater upper secondary coverts; the outermost is located between secondaries 1 and 2 and the innermost between secondaries 9 and 10. Just proximal to secondary 11 are three overlapping feathers; two of these appear to attach near the distal-most extremity of the humerus, whereas the other (the third) attaches beside the olecranon process of the ulna. This feather may therefore be the innermost lesser upper secondary covert. Otherwise, lesser upper secondary coverts are absent. Marginals cover the apterium anterior to the row of middle upper secondary coverts.

There are 10 lower greater primary coverts, each attached proximal to its corresponding primary, and a second row of 10 coverts that presumably are lesser under primary coverts (Pitelka 1945:232; Mewaldt 1958). Anterior to the 10th lesser under primary covert in some individuals is a very covert-like feather. This may be a displaced marginal. There are seven or eight lower greater secondary coverts attached proximal to the bases of the corresponding first seven or eight secondaries. As in *Nucifraga* and *Aphelocoma*, these are small down-like feathers. Of the nine lower middle secondary coverts, the first is located between secondary 1 and primary 1 and the last, or innermost, between secondaries 9 and 10. There appear to be 10 lesser under secondary coverts. The outermost is proximal to secondary 1 and the innermost is anterior to secondary 10. A laterally displaced feather attached at the base of primary 1 apparently is the feather considered by Pitelka (1945) to represent the distal-most covert of the lesser under secondary covert series. If this is the case, *Gymnorhinus* possesses 11 lesser under wing coverts. The lower marginal coverts are long, soft feathers sparsely covering the wing proximal to the metacarpal region.

Caudal tract. There are 12 rectrices; the center pair (1-1) is displaced dorsally. Fully developed upper tail coverts apparently corresponding to rectrices 2-6 are present; the center pair is represented by small downy feathers. The principal row of under tail coverts also numbers 10. However, here it appears that it is pair 6 rather than pair 1 that is lost. There is a second row of 10 under tail coverts plus up to 20 smaller feathers enclosing an apterium just posterior to the anal circlet. The anal circlet is composed of two to three poorly defined rows of dull white feathers incompletely circumscribing the vent. The vent usually is enclosed anteriorly.

Capital tract. In *Gymnorhinus*, as in *Aphelocoma* and *Nucifraga*, two apteria are present. The temporal apterium, the main portion of which is located posterior to the eye and dorsal to the auricular region, extends to the commissural point. The postauricular apterium is almost continuous with the lateral neck apterium. The eye appears to be encircled by a complete inner circle of feathers plus an incomplete outer circle. The postero-ventral margin of the ear opening is enclosed by one or two rows of feathers. Pitelka (1945:230) states that this is the case also for *Aphelocoma*. However, our investigation of a fresh specimen of *A. c. woodhouseii* from New Mexico

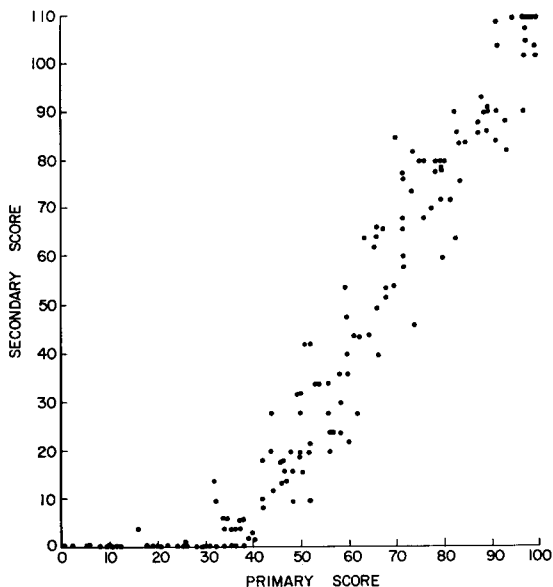


FIGURE 1. Secondary score in relation to primary score in molting adult Piñon Jays. See text for methods of scoring.

revealed three rows of feathers in this region. *Nucifraga* also possesses three rows (Mewaldt 1958, and confirmed in the present study). Feathers from the loreal region extend over the nostrils in many corvids. These are absent in *Gymnorhinus* (as the name implies). Instead, the feathers posterior to the nares are short and bristle-like.

Humeral, femoral, and crural tracts. These are typical in *Gymnorhinus*, showing no deviation from the standard passerine pattern.

Spinal tract. The interscapular region is five to seven feathers broad; each row in the cervical region has about two more feathers. A middorsal apterium is present in the dorsal region as in *Nucifraga* (see Mewaldt 1958: fig. 1); antero-lateral to this apterium each segment of the dorsal region is about eight feathers broad. The postero-lateral margins of the middorsal apterium are composed of a single row of feathers. In the posterior pelvic region, a single large covert-like feather attaches to an elevated fold of skin which extends to the uropygial gland.

Ventral tract. The interramal region does not reach the posterior portion of the lower mandible. A sternal-marginal apterium, located between the dorsal and ventral marginal coverts of the wings and adjacent to the sternal region of the central tract, is present. As in *Nucifraga* and *Aphelocoma*, the sternal region is far broader than the abdominal region. The axillar region extends from the postero-lateral margin of the sternal region.

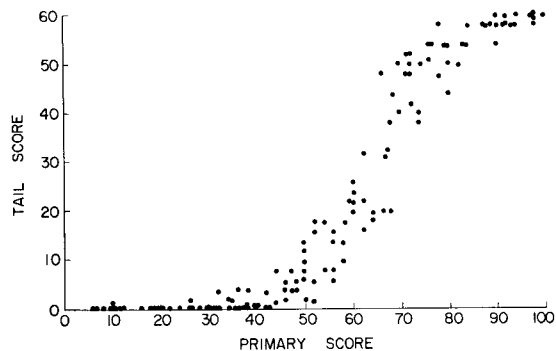


FIGURE 2. Tail score in relation to primary score in molting adult Piñon Jays. See text for methods of scoring.

It is composed of about 10 feathers and may be rather poorly defined.

THE ANNUAL MOLT IN ADULT AND FIRST-YEAR BIRDS

Primaries and secondaries. Molt begins with the first primary and continues on in sequence through primary 10. Typically, molt of equivalent primaries in each wing is closely synchronized. The number of primaries growing simultaneously ranged from 1 to 5, with the latter number being unusual.

The first secondaries to be shed are numbers 9, 8, and 1, in very close order. Secondaries 10, 2, 7, 11, 3, and 4, in about that order, are replaced next, with 5 and 6 being the final remiges to complete growth. With a single exception, the first secondary to be shed was not dropped until the fourth primary was molted, as in *Aphelocoma* (Pitelka 1945). Table 1 gives the mean number of growing primaries and secondaries for birds at different stages of molt, together with details on the molt of individual feathers.

Once secondary molt began, it progressed about twice as rapidly as primary molt throughout the molt of the remiges (fig. 1). The pattern thus shown for the Piñon Jay differs from that of the Bullfinch (*Pyrrhula pyrrhula*) (Newton 1966), where rate of secondary molt was at first slow, with an abrupt increase toward the end of the overall molt. In the Piñon Jay, secondary molt ended before primary molt in some fall-breeding individuals in which molt had been temporarily arrested.

Rectrices. The 12 rectrices are about as long as the four innermost primaries. Tail score was plotted in relation to primary score (fig. 2). Replacement of the rectrices often began soon after the fourth primary was molted and was almost complete as primaries 9 and 10 were growing. Up to four pairs of

TABLE 1. The molt of primary and secondary feathers in the Piñon Jay.

Molt stage	Remex score	No. of birds examined	No. of birds with the following feathers in growth																		Mean no. of growing primaries	Mean no. of growing secondaries										
			Primaries						Secondaries						1	2	3	4	5	6			7	8	9	10	11					
1	2	3	4	5	6	7	8	9	10	1	2	3	4	5							6	7						8	9	10	11	
1	1-10	6	6	6	3																					2.5						
2	11-20	7	7	7	5																						2.7					
3	21-30	10	8	9	10	6																					3.3					
4	31-40	18	3	4	16	18	5	1													2				4	10	1	2.6	0.9			
5	41-50	20	1	3	15	20	10														17	1			1	19	17	11	2.5	3.3		
6	51-60	19				1	17	19	7												18	8	1		1	18	9	10	4	2.3	3.6	
7	61-70	16					2	14	15	3											4	14	6		3	8	1	9	13	2.1	3.6	
8	71-80	17								3	16	17	5										8	17	5		9	1	1	12	2.4	3.1
9	81-90	11								4	9	11	9										2	6	9	6	4	6	1	3	3.1	3.4
10	91-100	6																					1	1	4	4	4	2		1	3.2	2.7
11	101-110	3								2	3	3	3																		3.7	1.7
12	111-120	3								1	2	2	2																		1.7	1.7

TABLE 2. The molt of the body feathers and small feathers of the alar and caudal tracts of adult Piñon Jays in relation to remex molt.

Feather group	Stage of remex molt												
	1 (6) ^a	2 (7)	3 (10)	4 (18)	5 (20)	6 (21)	7 (15)	8 (17)	9 (7)	10 (7)	11 (5)	12 (3)	12+ (11)
Upper greater primary coverts	6	7	10	18	20	21	15	17	7	7	3		
Upper greater secondary coverts		1	7	18	7	3							
Lower greater primary coverts						6	6	16	7	6	5	1	
Lower greater secondary coverts						6	7	14	5	6	5	1	
Marginal coverts	1	3	4	15	19	20	12	14	6	4	1	1	
Alula							2	15	5	3	1		
Capital tract					8	15	15	17	7	7	5	3	1
Spinal tract		1	5	14	20	21	15	17	7	7	5	3	10
Ventral tract		1	4	13	20	20	15	17	7	7	5	3	8
Humeral tract		1	4	14	20	20	15	17	7	7	5	3	4
Femoral tract		1	5	13	20	20	15	17	7	7	5	3	5
Crural tract			1	13	20	15	15	15	6	7	3	1	
Upper tail coverts				6	15	18	13	13	4	2	1	1	
Under tail coverts				5	14	18	15	15	5	2		1	

^a Total no. of birds examined in parenthesis.

rectrices frequently were growing concurrently. Most birds in stages 4 and 5 and all in stages 6 to 9 had growing rectrices.

Two specimens show asymmetrical molt that possibly is not due to accidental feather loss. Their abnormal condition is as follows: (1) rectrices 1 and 2 on both sides replaced, 3-6 left-old, 3 right- $\frac{3}{5}$ grown, 4 right- $\frac{1}{2}$ grown, 5 right- $\frac{2}{5}$ grown, and 6 right- $\frac{1}{5}$ grown; (2) 1-6 left-new, 1 right- $\frac{3}{5}$ grown, 2 right- $\frac{1}{2}$ grown, 3-6 right-old.

Body plumage. Table 2 shows the timing of molt of the other feather tracts in relation to molt of the primaries plus secondaries 5 and 6. Molt continues beyond replacement of all remiges in several of the body tracts. For example, 10 of 11 birds examined after the end of remex molt and before 1 January showed molt in the spinal tract.

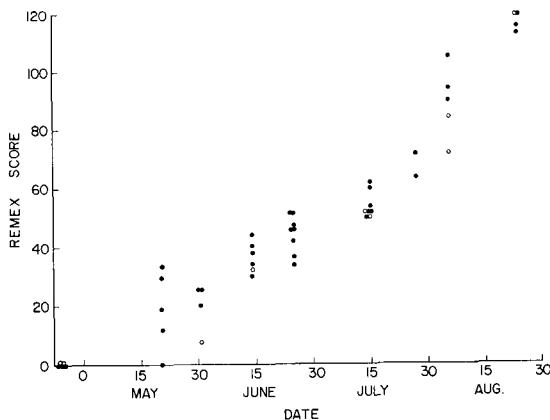


FIGURE 3. Remex score in relation to date in adult Piñon Jays taken from the Magdalena flock in 1970. Dots represent males; open circles represent females.

The upper greater secondary coverts are dropped almost simultaneously before any secondaries are lost. However, each upper greater primary covert is dropped with its corresponding primary.

TIMING AND RATE OF ADULT MOLT

Regression analyses of molt scores on date were made for each sex, population, and year. For example, adult males taken in 1970 from the Magdalena flock were compared with adult females taken at the same time and place (see fig. 3). With only one exception (see below), all *b* values (slopes or rates of molt) were statistically similar. Two aspects of onset and timing of molt became clear as a result of these analyses. First, in the El Morro sample from 1969, the only one which contained enough immature birds for comparisons with adults, onset of molt in the four categories (adult and immature males, adult and immature females) differed. Figure 4 illustrates that immature males began the molt

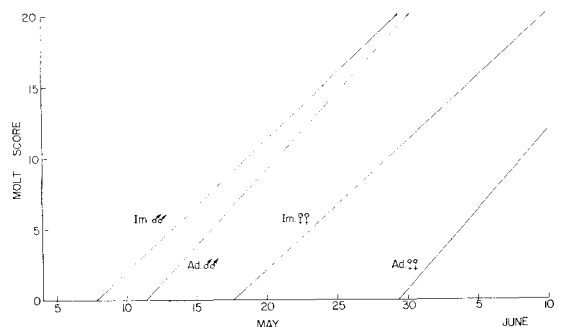


FIGURE 4. Linear regression lines of molt score against date for yearling and adult Piñon Jays taken from the El Morro flock in 1969.

slightly earlier than other groups, followed by adult males, then immature females, and last, the adult females (see table 3). Five birds collected from the Magdalena flock on 25 June 1969 suggest a similar picture: two adult males—molt score 22 and 12; adult female—molt score 0; immature male—molt score 42; and immature female—molt score 32.

The calculated slope for adult females from El Morro differed significantly from that of adult males taken from the same flock in the same year ($t = 5.78$, $P < 0.01$), but not from those of immature birds of either sex. The late start of molt in the few adult females collected probably is a result of delayed breeding. Neither of two collected on 29 May had started to molt; at least one of these was incubating fresh eggs. No first-year female collected had bred.

The second relationship indicated is that onset of molt is influenced by previous events. In the Magdalena flock, molt began earliest in 1970 when breeding was very early. It was next earliest in this population in 1972 when some spring breeding occurred and was

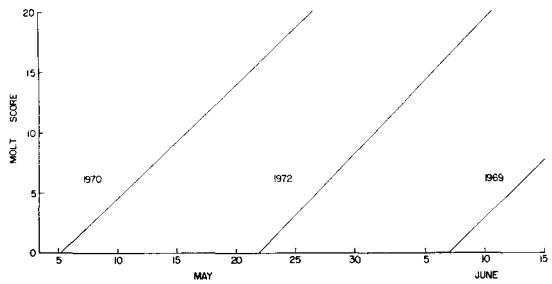


FIGURE 5. Linear regression lines of molt score against date for adult male Piñon Jays from the Magdalena flock in 1969, 1970, and 1972.

very late in 1969 when spring breeding did not occur (see table 4 and fig. 5). Conditions were so unfavorable in 1971 that the jays did not breed at all. The few birds collected suggested that molt began late in at least some individuals. Two adult males and an adult female taken on 3 June had not started to molt.

These data indicate that time of breeding and whether or not it takes place at all within a given year influence the initiation of molt.

TABLE 3. Estimates of rate, duration, and timing of molt in Piñon Jays from the El Morro flock using regression analysis.

	Ad. ♂♂	Ad. ♀♀	Im. ♂♂	Im. ♀♀
Sample size	22	5	11	9
Regression equation	$y = -11.85 + 0.859X$	$y = -33.3 + 1.14X$	$y = -7.06 + 0.890X$	$y = -16.18 + 0.910X$
Rate increase in primary score (points/day)	0.859	1.140	0.890	0.910
Calculated duration of remex molt (days)	154	135	143	150
Calculated start of molt	15 May	30 May	9 May	19 May
Correlation coefficient, $r(P)$	0.92 ($P < 0.01$)	0.97 ($P < 0.01$)	0.96 ($P < 0.01$)	0.95 ($P < 0.01$)

TABLE 4. Estimates of rate, duration, and timing of molt in adult male Piñon Jays using regression analysis.

	El Morro 1969	Magdalena ^a 1969	Magdalena 1970	Magdalena 1972
Sample size	22	8	34	15
Regression equation	$y = -11.85 + 0.859X$	$y = -36.3 + 0.960X$	$y = -4.71 + 0.909X$	$y = -22.4 + 1.1X$
Rate of increase in primary score (points/day)	0.859	0.960	0.901	1.1
Calculated duration of remex molt (days)	154	142	137	130
Calculated start of molt	15 May	8 June	6 May	21 May
Correlation coefficient, $r(P)$	0.92 ($P < 0.01$)	0.97 ($P < 0.01$)	0.95 ($P < 0.01$)	0.88 ($P < 0.01$)

^a Only birds taken through 20 August are included.

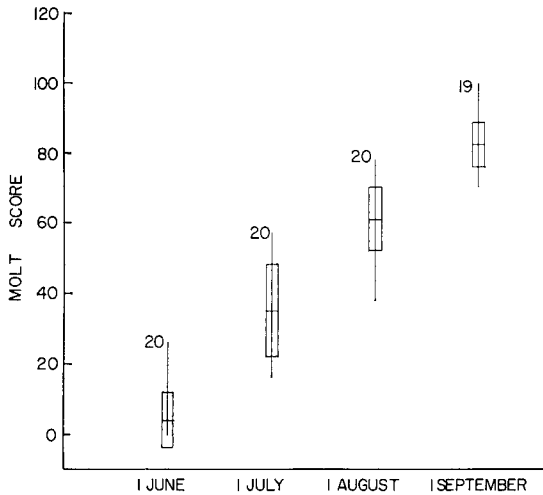


FIGURE 6. Molt scores of captive adult male Piñon Jays at one month intervals. For each date the mean (vertical horizontal line), range (vertical line), SD (rectangle), and sample size are shown.

In addition, they suggest that onset of molt is related to age, with nonbreeding immature birds beginning to molt before adults of the same sex, presumably as a result of less inhibition of the molt by hormones associated with reproduction (see also Balda and Bateman 1971).

The captive male Piñon Jays were spatially isolated from females, thus their relevant reproductive histories were identical. Nevertheless, considerable variation existed in molt scores on a given date (fig. 6). This could be attributed only to individual variation in gonadal regression and its effects on molt (see next section). There was no significant difference in rates of molt between 1 June and 1 July, nor between 1 July and 1 August. However, between 1 August and 1 September, the rate of molt slowed significantly (paired $t = 3.30$, $P < 0.01$) (table 5).

RELATION BETWEEN TESTES REGRESSION AND MOLT

Piñon Jays show a correlation between regression of the testes and molt score. Regression analysis of log testes volume against molt score in wild-taken birds shows a high cor-

TABLE 5. Rate of molt in captive adult male Piñon Jays.

	1 June— 1 July	1 July— 1 August	1 August— 1 September
Number	20	19	19
Mean rate (points/day)	0.909	0.847	0.664
SD	0.313	0.259	0.149

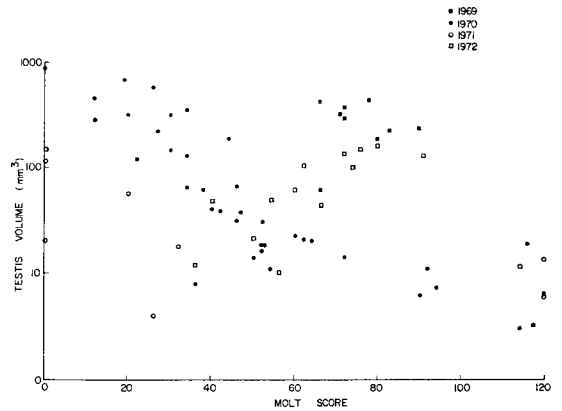


FIGURE 7. Testis volume versus molt score in adult male Piñon Jays taken from the Magdalena flock.

relation ($r = 0.76$, $P < 0.01$) between decrease in testis size and increase in molt score (fig. 7). However, there are exceptions to this relationship. In most males taken from the Magdalena flock in mid-August 1969 and in early August 1972, testes were fully developed or were enlarging, apparently in response to green piñon seeds or cones (Ligon 1971 and unpubl. data). Thus, the gonads have the capability to enlarge in at least some individuals, even though the birds are actively molting. In short, environmental stimuli can trigger full gonadal development in molting jays. If this occurs, molt may be arrested until a nesting cycle is completed (Ligon 1971).

A similar relationship between testes regression and molt score was found in the captive males studied. Testes volume decreased with increase in molt score in birds examined on 1 June, 1 July, and 1 August ($r = 0.77$, $P < 0.01$). This relationship was obscured if data from 1 September were included in the analysis.

MOLT AND LATE SUMMER BREEDING

Ligon (1971) outlined the relationship of molt and late summer breeding in the Magdalena flock. Molt was suspended in breeding birds, but was completed after the young fledged. Figure 8 illustrates the suspension of molt in adult Piñon Jays from the time breeding began (about 19 August) until after the young fledged in mid-October. Molt continued through ovulation in at least some individuals, as a female collected after she had completed her clutch was molting. In contrast, in another passerine, *Zonotrichia capensis* of Peru, an incipient molt was arrested by the onset of breeding and was not resumed following completion of reproductive activity (Davis 1971).

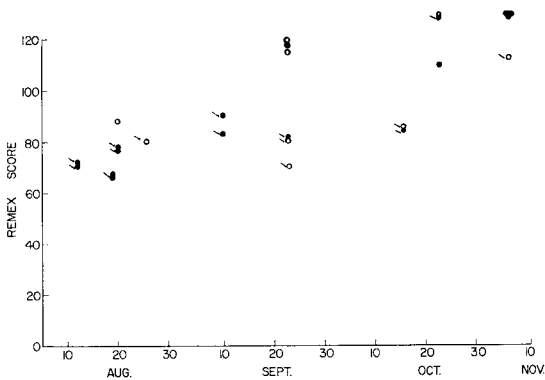


FIGURE 8. Remex score in relation to date in adult Piñon Jays taken from the Magdalena flock in 1969, when late summer breeding was initiated. Checks indicate probable breeders as based on testis size, brood patch development, and/or behavior. Dots represent males; open circles represent females.

INTEGRATION OF MOLT AND REPRODUCTION

Breeding occurred in the spring of each year in the El Morro flock; the exact timing varied with weather and food conditions as described by Balda and Bateman (1972) for the Piñon Jays they studied. However, variation in the annual cycle during the 4-year period 1969–72 was great in the Magdalena flock. A brief description of the relationship between breeding and molt in each year follows.

1969. Successful reproduction did not occur in the spring. Onset of molt was very late; it had barely begun in late June. In mid-August breeding activity commenced in about a third of the flock of 300 jays, concurrent with maturation of a huge crop of piñon seeds. Molt was arrested in breeding birds until the young were fledged (Ligon 1971).

1970. The piñon seed crop of the previous autumn provided abundant food through the winter and early spring, allowing breeding to begin in early February. Nesting and re-nesting (as a result of failure of earlier nests) persisted through June. In many individuals molt began in early May, presumably in those which bred early and successfully. Although the summer rains produced more vegetation in late summer and autumn, and correspondingly more insects, than in 1969, there was no indication of late summer gonadal resurgence. No piñon seeds were produced.

1971. This was a very dry year in New Mexico. Spring breeding did not occur, and in fact the jays remained in large (ca. 100), roving flocks throughout the spring. Molt in the few specimens obtained began about a month later than in the previous year, but earlier than in 1969. Again no piñon seeds

were produced and no evidence of autumnal sexual activity was recorded. No reproduction occurred in 1971.

1972. A wet spring, together with a massive emergence of cicadas, permitted some breeding in late spring. Molt was later than in 1970, but earlier than in 1969 (fig. 5). In August, piñon cones were present on a minority of trees (ca. 10%) and this, it appears, triggered gonadal development and sexual behavior in some molting jays (fig. 7). However, there was no evidence that successful nesting took place.

This phenology of reproduction and molt in the Magdalena flock allows a consideration of the relationship between these two major features of the annual cycle. As Payne (1972: 130) has pointed out, complete understanding of this relationship in wild birds does not exist, and mechanisms involved appear to vary from species to species, or even within species, e.g., *Z. capensis* (Miller 1961; Wolf 1969; Davis 1971; King 1972).

We assume, like Payne (1972:117), that hormonal interactions determine the timing of breeding and molt in the annual cycle. The year to year variation in breeding and molt shown by this population of Piñon Jays provides clues as to interactions between the proximate causal factors (hormones) affecting breeding and molt. Unpublished studies by Ligon show that long photoperiods stimulate gonadal development in the Piñon Jay. Thus, in this respect Piñon Jays are like typical temperate-zone passerines. However, the jays also can develop enlarged gonads and breed in fall in response to special environmental stimuli (abundant green piñon cones) (Ligon 1974). Thus, it is apparent that gonadal development can result from more than one kind of environmental cue.

Molt in many bird species is influenced by gonadal hormones or gonadotropins (Payne 1972:117), and this appears to be true also of the Piñon Jay. However, this interaction is not simple or absolute. Our interpretation of this interrelationship is as follows.

1. Gonadal hormones influence onset of molt. In 1969, when breeding did not occur in spring, the gonads probably retained their competence and initiation of molt was delayed. In 1970, breeding was early, as was molt. In 1972, spring breeding occurred later than in 1970; likewise, molt was later. These observations agree with those of Payne (1969: 66): birds which breed early, molt early.

The situation in 1971 is of special interest. Spring breeding did not take place. Environmental conditions apparently were so un-

favorable as a result of the drought of that year that gonadal competence was not retained and, upon regression of the gonads, molt began in early June. We interpret this gonadal regression by early June, in the absence of breeding, as response to highly unfavorable environmental conditions. This, in turn, allowed molt to commence earlier than otherwise would have been the case (cf. 1969).

2. It also is apparent that the supposed influence of the gonads on molt has limitations. In 1969, molt occurred, albeit late, despite a probable persistence of gonadal readiness. It appears that, at some point in early summer, factors which serve to stimulate molt (possibly photoperiod) override the inhibiting effects of gonadal hormones. It is further probable, but unproved, that gonadal activity decreases to some extent at this time. Waxing and waning of the gonads without complete regression or a period of refractoriness is known for another temperate-zone passerine, the Great-tailed Grackle (*Cassidix mexicanus*) (Selander and Hauser 1965).

3. Finally, recrudescence of the gonads to full breeding condition in August 1969 caused a complete arrest of the molt, illustrating the inhibitory effects of reproductive hormones on molt. Following breeding, molt is resumed and completed (Ligon 1971).

These facts indicate that in the Piñon Jay, as in many other temperate-zone passerines, there is a tendency for separation of two major events of the annual cycle, breeding and molt. This separation appears at least in part to be accomplished by gonadal inhibition of molt (see Payne 1972:110). In a species or population with unpredictable breeding patterns such as the Piñon Jay, one might expect this separation to be imperfect, and this is the case. Many variations exist on the breeding-molt theme (Payne 1972:131), and these depend on the particular ecological setting and pattern of life of the species in question. Piñon Jays of this region appear in some respects to be intermediate between "typical" temperate-zone passerines and certain Old World desert species which molt in a predictable manner, but which breed opportunistically at any time, as suitable environmental conditions become available. These jays live in the temperate zone with its distinct seasonality, including predictable summer rains (see Ligon 1971:fig. 2) and subsequent abundance of insect foods; however, the unpredictable spring weather (wet or, usually, dry; warm or cold) and food supply at that time, and particularly the unpredictable crops of piñon seeds, provide selective advantage for

opportunistic breeding similar to that seen in certain desert areas where rainfall and the resultant food supply occur unpredictably in time and space (e.g., Immelmann 1963).

Payne (1972:144) points out that molt is far less expensive metabolically than breeding, and that it typically occurs during the warm part of the year, further reducing its cost. Additionally, in the Piñon Jay, insects are the major food during the molt (Ligon, unpubl. data, based on stomach contents of all specimens taken), providing protein necessary for feather development (Payne 1972:144). Although molt may be relatively inexpensive metabolically, it appears nevertheless to be incompatible with breeding. The energy saved by scheduling these two events separately thus must be of importance in the Piñon Jay.

FACTORS INFLUENCING ONSET OF MOLT

Proximate factors are the cues used in the timing of events such as the annual molt. In the absence of experimental data, one must resort to evaluation of circumstantial evidence in identifying such cues.

Photoperiodism probably is involved in initiation of molt in adult Piñon Jays. Support for this assumption follows. (1) Gonads of Piñon Jays are responsive to experimental manipulation of photoperiod, i.e., the birds are photosensitive (Ligon, unpubl. data). (2) Photoperiod is the only consistent environmental cue available to the jays. (3) Onset of molt is far more predictable from year to year than is breeding. (4) Four yearling Piñon Jays exposed to 18-hr periods of light began a complete molt in December, about 5 months earlier than it would have occurred in nature. This molt was largely normal, but was somewhat accelerated as compared to molt of captives on natural photoperiods, presumably as a result of the very long periods of light.

Although photoperiod may be the fundamental cue involved in initiation of molt, it is obvious that other factors, such as hormones associated with breeding activity, modify this timing in the Piñon Jay populations we studied. The relationship between food supply and breeding and between time of breeding and onset of molt was described earlier.

Summarizing, onset of molt in Piñon Jays appears to be influenced by photoperiod and may be modified either (1) directly, by a shortage of food, which also suppresses breeding, or (2) indirectly, by food shortage which retards or prohibits breeding, with this, in turn, delaying the beginning of molt.

TABLE 6. Arbitrary stages of postjuvinal molt in the Piñon Jay.

Stage 1.	Molt has begun on the upper marginals and lesser coverts and on the sternal portion of the ventral tract; feather growth continues on the spinal tract and sometimes on femoral and crural tracts.
Stage 2.	Molt has begun on all major tracts of the body, plus the middle upper secondary coverts. A few blue feathers are present in the capital tract.
Stage 3.	Molt of interramal and submalar regions is heavy. New blue feathers of capital tract are becoming conspicuous. Middle upper secondary coverts are mostly grown. Greater upper secondary coverts are growing (if replacement of these occurs), or are in some cases grown. Some juvenal upper tail coverts usually are still present.
Stage 4.	Molt of upper and lower tail coverts is heavy. Molt of middle secondary coverts is complete, as is greater secondary covert molt (if it occurs). Molt of head feathers is virtually complete.
Stage 5.	Overall appearance is blue. Many feathers of both dorsal and lateral portions of the capital tract are still ensheathed at bases, as are some feathers in other tracts.
Stage 6.	Molt is complete.

POSTFLEDGING DEVELOPMENT OF JUVENAL PLUMAGE AND POSTJUVENAL MOLT

Piñon Jays hatch without down, as do jays of the genera *Aphelocoma*, *Cyanocitta*, and *Cyanocorax*, in contrast to *Nucifraga* and *Corvus*, in which newly hatched young possess down. Development of nestling Piñon Jays is described in detail by Bateman and Balda (1973).

Development of juvenal plumage. Active feather growth (development of juvenal plumage) is still in progress in most or all feather tracts at fledging and continues for some time thereafter. All 10 primaries and at least 10 secondaries (1-10) are growing, as are the greater upper primary and secondary coverts. The smaller dorsal coverts are well developed. Greater underwing coverts are absent at fledging, as also is true of *Aphelocoma* jays (Pitelka 1945) but not of Clark's Nutcracker (Mewaldt 1958). Marginal feathers along the lower anterior patagial membrane are growing heavily when the rectrices are half to two-thirds grown. Middle underwing coverts are grown by the time the greater coverts are in the brush stage.

Determination of onset of postjuvinal molt is difficult, as the last portion of juvenal plumage development, which produces pale blue feathers similar to those attained by the postjuvinal molt, overlaps in time with onset of the postjuvinal molt. For example, development of the under greater secondary coverts and growth of the rectrices may not be completed by the onset of postjuvinal molt. The last feathers of the juvenal plumage to appear are those of the lateral regions of the spinal tract, plus additional feathers in the loral, malar, and auricular regions. These feathers are a pale blue, in contrast to the remainder of the juvenal body plumage, which is dull gray, and are not so lax in texture. In short,

they appear similar to body feathers attained by the postjuvinal molt. The facts that (1) these feathers, particularly those of the spinal tract, appear not to be replacing older feathers; and (2) they appear before molt of the marginals begins (which signals onset of postjuvinal molt in most or all passerines studied) support the above interpretation. Pitelka (1945) describes production of adventitious adult-like blue feathers in juveniles of *Aphelocoma coerulescens*, "well before the beginning of the postjuvinal molt." He points out that this demonstrates a change in developmental physiology, i.e., juveniles are capable of producing blue feathers before the time of normal molt. We interpret the events described above for the Piñon Jay as evidence that physiology of feather development changes normally in this species before completion of juvenal plumage development.

Postjuvinal molt. This molt includes all body feathers and the small feathers of the alar and caudal tracts. In addition, replacement of some or all of the middle secondary coverts, greater secondary coverts, some secondaries, and, exceptionally, some feathers of the alula also were recorded.

Although external factors such as time of hatching influence the time of molt (e.g., age of the bird at its initiation), it was possible to devise an arbitrary system of molt stages into which the specimens examined could be placed, making possible an objective means of comparing molt between individuals (table 6).

The most striking variation in the pattern of molt occurred between spring- (February-June) and fall-hatched (September) birds (table 7). Only birds from the Magdalena flock were considered. No fall-hatched bird replaced any secondaries and no more than one replaced any greater secondary coverts,

TABLE 7. Molt of the alar tract in juvenile Piñon Jays from the Magdalena flock.

"Spring-Hatched" 1970.			Replacement of alar feathers		
Individual	Date collected	Molt stage	Secondaries	Greater secondary coverts	Middle secondary coverts
JDL 1127	7 August	5	8-11	all	all ^a
JDL 1130	7 August	5	7-11	all	all ^a
JDL 1131	7 August	3	none	8-9	all
JDL 1136	25 August	2-3	none	none	probably all
JDL 1137	25 August	5	7-11	all	all
JDL 1140	22 September	5	none	9-11	all
JDL 1141	22 September	5	9-11	4-11	all
"Fall-hatched" 1969.					
Number	Molt completed				
11	11		none	none ^b	from 0 to 6 replaced

^a Part or all of the alula feathers replaced in these two birds.

^b One immature collected 12/30/69 may or may not have been a fall-hatched bird. If so, it is the only one of 12 collected to show any replacement of greater secondary coverts (nos. 5-10).

whereas all spring-hatched birds replaced the latter to a greater or lesser extent. In addition, in 1970, the early hatched spring birds (as determined by molt stage on a particular date, see table 7) apparently replaced more feathers in the alar tract than did later hatched individuals (cf., for example, nos. 1136 and 1137, collected on the same date where zero and five secondaries had been replaced, respectively, table 7). Immatures from the El Morro flock (taken 1969-71) showed an intermediate situation, with from zero to three secondaries (one individual) and from one to eight (one individual) greater secondary coverts replaced. The El Morro flock did not breed as early as did the Magdalena flock in 1970, nor as late as it did in 1969.

Pitelka (1945) reported that in *A. coerulescens* more greater secondary coverts were replaced in southern than in northern populations. He postulates that, among other factors, timing of breeding might be involved. Data presented here for the Piñon Jay support this view. Food was abundant for the fall-hatched Piñon Jays, as it was for the spring-hatched birds in 1970; thus it appears that variation in number of feathers molted is controlled by other factors, such as photoperiod. It also is possible that type of food (insect in spring-hatched jays, mostly piñon seeds in fall-hatched birds) exerted an effect.

Fall-hatched birds began molting at about 45 days of age, whereas birds hatched early in 1970 (ca. 1 March) began the molt at about 60 days. Such acceleration of molt late in the year also is reported for the Bullfinch (Newton 1966).

Summarizing, it appears that Piñon Jays that hatch early may replace up to six secondaries and all greater and middle secondary

coverts, while birds that hatch later replace progressively fewer feathers of the alar tract. Fall-hatched birds replace no secondaries, few if any greater primary coverts, and only about half of the middle secondary coverts. Replacement of fewer feathers in later-hatched young also is known in several other passerines.

AGE DETERMINATION

Piñon Jays can be separated into three age categories (Juvenile; First-year, Immature, or Yearling; and Adult) by plumage characteristics. These plumage characters are clear-cut and reliable when used in combination. Similar characters used for age determination in other corvids have been described by Pitelka (1945), Emlen (1936), and Mewaldt (1958). In addition, features such as mouth color supplement methods of aging by plumage characters. Nomenclature of plumage colors follows Ridgway (1886).

Juveniles can be recognized by the following traits:

1. Juvenal body feathers are Mouse Gray with no hint of blue, except those which develop after fledging along the margins of the spinal tract and sometimes in the malar and auricular regions. Body feathers are lax or fluffy; i.e., they are distinctly less compactly formed than those of first year and adult birds, as reported by Bateman and Balda (1973).

2. There are few or no glossy blue feathers in the malar region.

3. The basal portion of the lower mandible may be flesh-colored for some time after fledging. This appears to be highly variable (R. P. Balda, pers. comm.).

4. The inside of the mouth is pinkish or white.

TABLE 8. Measurements^a of Piñon Jays by age and sex.

Measurement	Age and Sex	Number	Range	Mean	SD
Culmen length ^b	Adult males	47	31.2–38.0	35.34	1.65
	Adult females	23	30.8–36.5	33.18	1.50
	First-year males	8	32.0–36.8	33.73	1.59
	First-year females	4	31.9–35.0	32.88	1.45
Wing length ^c	Adult males	52	146.0–159.0	152.14	3.25
	Adult females	46	139.0–154.0	145.20	4.05
	First-year males	8	142.0–156.0	147.75	5.39
	First-year females	2	139.0–140.0	139.50	
Tail length ^c	Adult males	51	102.0–119.0	110.62	3.99
	Adult females	46	97.5–119.0	103.97	4.00
	First-year males	8	101.0–111.5	106.54	3.62
	First-year females	2	98.0–98.45	98.45	
Tarsal length ^d	Adult males	107	34.0–40.5	37.00	1.94
	Adult females	63	28.9–39.1	35.81	1.99
	First-year males	26	33.5–40.5	37.80	1.87
	First-year females	21	34.0–39.2	35.67	1.45

^a In millimeters.^b Taken only from birds collected 1 August–31 October from the Magdalena flock.^c Taken from birds collected 1 September–28 February from the Magdalena flock.^d Taken from all birds collected from Magdalena flock.

5. The rectrices are rounded or bluntly pointed; those of adults are truncate (Bateman and Balda 1973; present study).

6. The whitish throat patch of first-year and adult bird is lacking.

Following the postjuvinal molt, which includes neither the rectrices nor most of the remiges, Piñon Jays assume the gray plumage mentioned by Balda and Bateman (1971). This plumage overall is actually a pale blue, not matched in Ridgway (1886), and is easily distinguishable from the gray juvenal plumage. When fresh, it is sometimes very similar to fresh adult plumage. However, first-year birds can be recognized confidently in the hand as such until the end of the first complete molt by use of the following characters.

1. The retained remiges provide probably the most conspicuous cues as to age. Primaries and secondaries in first-year jays initially are a dark Clove Brown instead of blackish (Brodkorb 1936), and this difference becomes more conspicuous as the feathers age. By midsummer, when the first complete molt is in progress, the old (juvenal) remiges are Hair Brown and contrast strikingly with the new remiges. The last remex to be replaced, secondary 6, alone can indicate whether or not the bird is completing its first complete molt.

2. Other feathers usually retained from the postjuvinal molt, such as alular feathers, greater primary and greater secondary coverts, and sometimes middle secondary coverts, tend to be Drab Gray. These stand out in contrast to the replaced marginals and whatever other coverts that had been renewed.

3. Feathers of the loreal, malar, and auricu-

lar regions are a glossy Azure Blue, but are less deeply colored than those of adults. The whitish throat patch is present.

4. Mouth color still is largely white in the first-year birds.

The crown in adult Piñon Jays is a deep Cyanine Blue. The malar region is Cobalt or Azure Blue and the body is a paler Flax Flower Blue. Color change due to feather wear occurs. Freshly molted birds have pale loose barbs at the margins of the body feathers, giving the birds a somewhat grayish cast. By spring these have worn away, producing a deeper blue. Adults can be recognized as such by black, rather than brown, inner web of the primaries, distinctly blue rather than grayish blue outer webs. In addition, adults possess a black mouth lining. However, this character appears to be associated with reproductive condition as well as age. In adult females the posterior-most portion of the mouth is pale during the nonbreeding season, whereas it is black during periods of breeding. This was not noted in adult males, whose entire mouth linings were almost always black (Ligon, unpubl. data). Payne (1969:91, 94) showed a correlation between breeding condition and darkness of the mouth lining in the *Agelaius* blackbirds he studied.

MEASUREMENTS

Bill length measurements of adult male specimens taken from the Magdalena flock from August 1969 to July 1970 were analyzed by grouping measurements into four 3-month intervals. August was the first month of extensive use of piñon seeds. Culmen lengths did

not differ significantly between the August–October and November 1969–January 1970 specimens, nor between those taken February–April and May–July. However, the first three groups combined were significantly shorter ($t = 3.38$, $P < 0.01$) than those taken May–July 1970. Measurements for each interval are: August–October 1969 ($n = 14$, $\bar{x} = 34.70$, $SD = 1.84$); November 1969–January 1970 ($n = 17$, $\bar{x} = 34.05$, $SD = 1.46$); February–April 1970 ($n = 8$, $\bar{x} = 35.75$, $SD = 1.20$); and May–July 1970 ($n = 29$, $\bar{x} = 36.10$, $SD = 1.73$). This seasonal variation in bill length agrees in principle with the findings of Davis (1954) for Scrub Jays. We, like Davis, interpret this as a reflection of mechanical wear on the bill tip, caused by use of different foods. Beginning in August 1969 and continuing into spring 1970, these Piñon Jays fed largely on piñon seeds (Ligon, unpubl. data). The seeds were hammered open with the bill.

Table 8 shows measurements of each of four age and sex classes. Adult males were significantly larger than first-year males in wing and tail lengths, but not in bill or tarsal lengths. They were significantly larger than adult females in all measurements. Immature males were not significantly larger than adult females in wing or tail lengths, but were larger in culmen and tarsal lengths.

Jays from the El Morro flock were compared with specimens from the Magdalena flock of the same age and sex and taken at similar times. We found no significant differences in mensural characters.

SUMMARY

Pterylography of the Piñon Jay is similar to that of other New World corvids, except that 11 rather than 10 secondaries are present.

Linear regression analysis of molt score on date revealed two basic features of timing of molt. First, yearlings of both sexes begin the molt prior to their adult counterparts. Second, initiation of molt is influenced by the previous breeding pattern. If breeding is early, molt is early; if breeding is late or does not occur, molt is late.

A significant inverse correlation exists between testes regression and molt. However, in 2 years (1969 and 1972), gonadal development occurred during the molt. This appeared to be related to the presence of green cones of the piñon pine. Molt was suspended in those jays which bred August–October 1969.

Innermost secondaries are replaced in some individuals during the postjuvenile molt. This variation appears to be related to the time of

hatching. Fall-hatched birds replaced no secondaries or greater secondary coverts during the postjuvenile molt.

Age specific characters are described for juveniles, yearlings, and adult Piñon Jays. These characters are related to feather color and shape (principally of the alar tract) and to color of the mouth lining.

Adult male Piñon Jays are significantly larger than adult females in each of four measurements. They are larger than first-year males only in wing and tail lengths.

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