

# PRIMARY MOLT OF CALIFORNIA CONDORS<sup>1</sup>

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*Abstract.* Primary molt of the California Condor (*Gymnogyps californianus*) was studied intensively from 1982 through 1985, using repeated flight photographs of the remaining individuals in the wild population as a basis for most analyses. On the average, wild condors replaced 4.4 of the 8 emarginated primaries on each wing each year. The specific primaries molted were generally the ones missed in the previous year and were usually well-distributed among the eight possibilities, with a tendency for low-numbered primaries to molt earlier than high-numbered primaries. Within individuals, molt of one wing was commonly very different from that of the other wing. Primary molt of captive juveniles was similar to that of wild juveniles.

The interval from loss to full replacement of individual primary feathers was normally 3½ to 4 months, with the primaries closest to the leading edge of the wing growing most slowly. Most primaries were shed between 1 February and 1 September. Primaries lost in late fall and early winter were not replaced until the following summer, indicating interrupted molt over the winter.

In general, primary molt of the condor differs from that of smaller cathartids in being highly seasonal, highly variable in sequence, highly asymmetric between wings, and in following a roughly 2-year cycle. Molt of the condor shows many similarities to that of the White Stork (*Ciconia ciconia*) and to that of large accipitrid vultures.

*Key words:* California Condor; *Gymnogyps californianus*; primary molt; secondary molt; rectrix molt.

## INTRODUCTION

In late 1981 we began intensive efforts to photograph wild California Condors (*Gymnogyps californianus*) in flight as a means of identifying individuals and censusing the remnant population. The many differences in feather patterns, especially primary feather patterns, proved diagnostic in differentiating individuals and led to minimum population counts of 21, 19, 15, and 9 wild condors for 1982, 1983, 1984, and 1985, respectively (Johnson 1985, Snyder and Johnson 1985). Identifying individuals through time required an understanding of patterns and rates of primary molt. Here we present the results of primary molt studies of wild individuals followed from 1982 through 1985, supplemented by data

on primary, secondary, and tail molt of captive condors studied in 1984 and 1985.

## METHODS

California Condors in full feather have 8 emarginated primaries (numbers 3 through 10) and two secondary-like primaries (numbers 1 and 2) on each wing (Fig. 1A). Because the emarginated primaries overlap only minimally and can be readily differentiated in flight photographs of wild birds, it has been possible to obtain comprehensive documentation of their patterns of molt through repeated photographs of individual condors. To facilitate systematic studies, the thousands of condor flight photographs taken in the past few years were sorted into files for individual birds and arranged in temporal sequences within each year. For each individual, we first tabulated the status of all primaries 3 through 10 for each date. We then determined the sequences in which

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feathers molted, the frequencies with which given primaries molted over the several-year period, and the maximum and minimum spans of time each molting primary took from loss to full replacement. Maximum replacement period was computed as the interval between the date an old primary was last photographed in place to the date a replacement feather was first documented photographically to be fully grown. Minimum period was computed as the interval between the date a primary was first photographed missing and the last date its replacement was photographed in less than fully developed condition. Normally there was no difficulty in determining the timing of loss of primaries, but we sometimes encountered problems determining when growth of a primary was finished. Judgments of the degree of completion of growing feathers were made by comparisons with lengths of adjacent feathers, but such judgments were sometimes hindered by problems with resolution of photographs, effects of angular aspect in the photographs, the fact that adjacent feathers were also sometimes growing simultaneously, and intrinsic variability in appearance of feather lengths, apparently due to momentary movements of feather tips in the wind. Thus, some of the variability in documented replacement periods undoubtedly traced to errors in judgment of completion dates. Some feathers, when complete, were abnormally short relative to adjacent feathers, but this was easily detected by looking at long series of photographs of individual birds and did not cause general difficulties.

Unfortunately, molt patterns of secondaries, rectrices, and primaries 1 and 2 could not be studied comprehensively by the photographic method, mainly because these feathers overlap one another to such an extent that patterns of loss and regrowth of specific feathers could not be discerned clearly at the usual distances from which photographs were taken. Nevertheless, we gained limited information on molt of these feathers from some of the better photographs of wild birds. In addition, we accumulated considerable data on molt of these feathers from annual fall examinations of captive condors at the Los Angeles and San Diego zoos. Captives were sometimes examined in the hand, but were more usually checked with binoculars while they were in sunning postures. Viewed at close range, feathers of the year were characteristically black and clean-edged, and were readily differentiated from

browner and more frayed feathers of previous years, allowing determinations of overall annual molt patterns.

However, annual inspections did not yield detailed information on molt sequences within years. Partial information on within-year sequences of captives was obtained in 1985 by periodic collection of molted primaries in the cages of three 2-year-old individuals. Not all primaries were recovered, but enough were found to allow some preliminary conclusions.

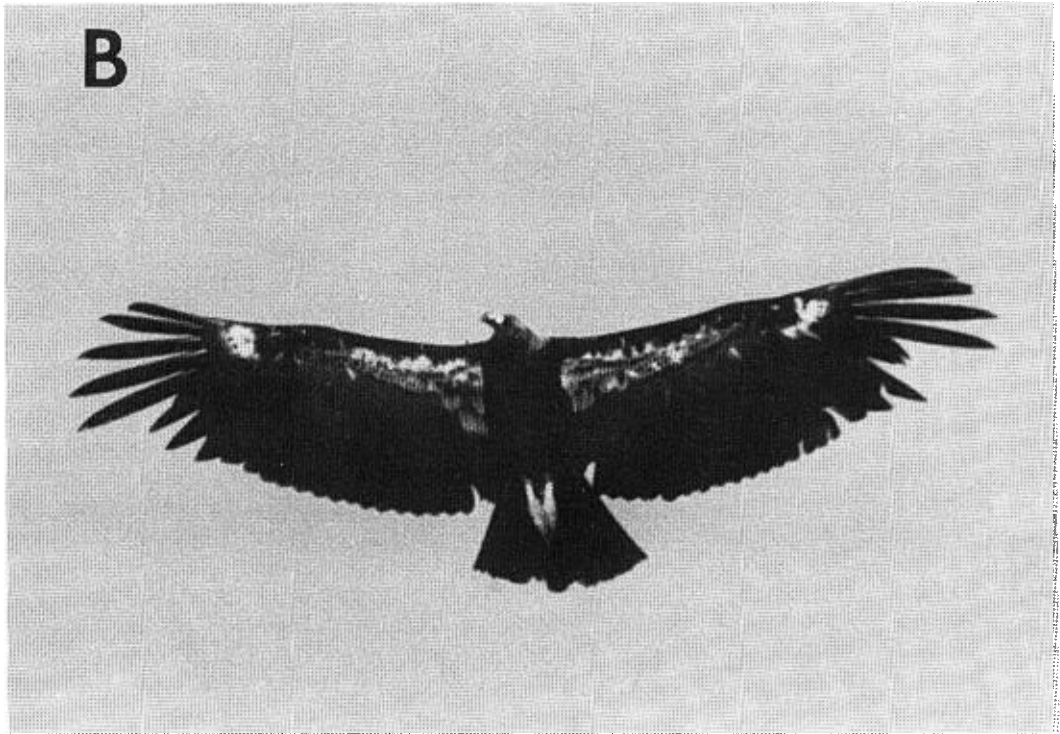
## RESULTS

### MOLT SEQUENCE AND FREQUENCY

The primary molt sequences of the 16 wild adults and seven wild immatures that were photographed during the 4-year period are presented in Table 1. From the temporal spacing of photographs and data on the time it takes individual primaries to complete loss-replacement cycles, we rated the molt data for each bird in each year as complete (all molting primaries detected), probably complete, or probably incomplete. For most of the analyses that follow, we used data only from birds and years for which we judged our information to be complete or probably complete.

Although molt sequences tended to be highly variable, an underlying pattern of low-numbered primaries molting before high-numbered primaries was discernible when the rank orders of primary molt were averaged for all wild adults and immatures (Table 2). In fact, the average rank orders show a perfect correlation with primary number by a Spearman's rank correlation test ( $r_s = 1.0$ ,  $P < 0.001$ ). This same relationship is apparent from an examination of the seasonal timing-of-loss distributions of the various primaries (Fig. 2).

Molt sequences were most regular in juveniles, which tended to replace primaries 1 through 5 in their first molting period, both in the wild and in captivity (see Todd and Gale 1970). However, several individuals did not progress as far as primary 5, some progressed farther, and in some, primary replacement did not proceed in a strictly consecutive order up the sequence (Tables 1 and 3). At one extreme was a wild bird (PAX) trapped and examined in the hand in late 1982, that molted only primaries 1 and 2 on one wing and primaries 1 through 3 on the other wing in his first molt. At the other extreme were two captives,



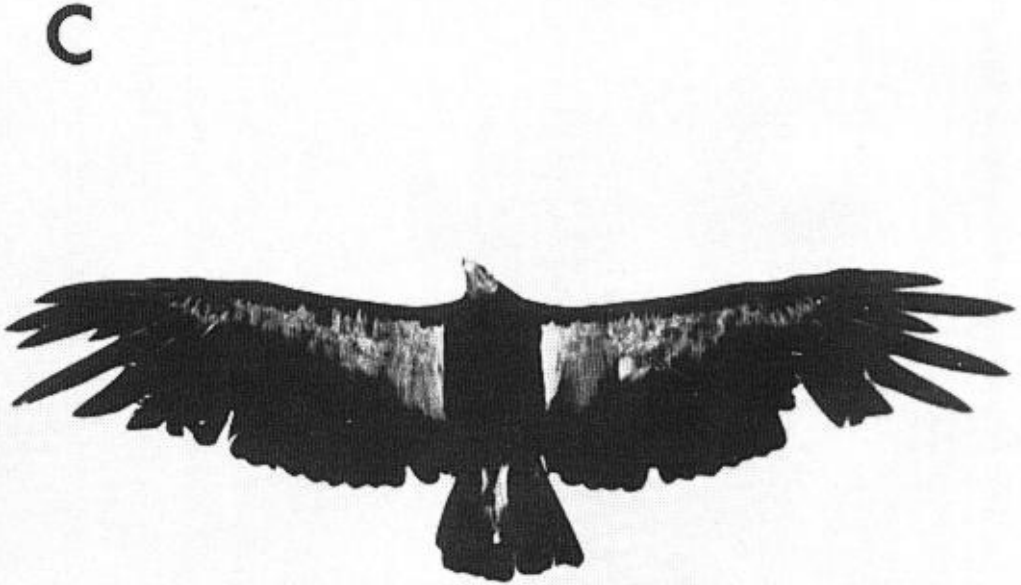


FIGURE 1. A. An adult California Condor (CCF) in perfect feather on 24 January 1982. Numbers indicate the emarginated primaries followed intensively in this study. B. Photograph of BOS toward the end of her first molting period on 2 September 1983, illustrating primary molt limited to lower-numbered primaries, and molt of innermost secondaries and rectrices. Note also secondary 1 on left wing clearly in molt and that sequence of replacement of primaries is normal on right wing but partially reversed on left wing. C. PCA in extremely heavy primary and secondary molt on 8 August 1983. Primaries in molt are L3, L6, L7, L9, L10, R4, R6, R7, and R8.

Tecuya and Piru, that molted primaries 1 through 7 on each wing during their first molts. In part, the number of primaries molted in the first molt was related to hatching date (Fig. 3), with the earliest-hatching birds molting the most primaries in the following year ( $r_s = -0.77$ ,  $P < 0.01$ ).

All three recent captives for which molted primaries were collected during their second molt (Almiyi, Tecuya, and Sisquoc) started their second molt by replacing primaries 1 through 3 for a second time. Partway through this process they also began replacement of high-numbered primaries they had not molted (or presumably had not molted) in their first year. For example, Almiyi, who had molted primaries 1 through 5 in her first molt in 1984, again dropped primaries 1 through 3 between February and April 1985, and in the same year also molted primaries 6 through 10, starting in April. The overall molting patterns of Sespe, Cuyama, Cachuma, and Topatopa in their second years suggested a similar

course of events, although the degree to which various captives began second molt waves up the sequence before they finished first waves was variable. At one extreme, Sisquoc and Tecuya molted primaries 1 through 4 as well as high-numbered primaries on both wings in their second molt periods. At the other extreme, Topatopa, the captive studied by Todd and Gale (1970), limited primary replacement in his second molt almost exclusively to high-numbered primaries and started a second molt wave only on one wing and only with primary 1.

Of the wild immatures, REC molted mainly high-numbered primaries in his second year, although photographs are adequate to show that he also molted primary 2 on both wings. It seems likely that he may also have molted primary 1 on both wings in this year, but this cannot be discerned clearly in the photographs. In his fourth year, REC again showed a molting pattern very similar to that of many captives in their second

TABLE 1. Sequences of primary feather molt in all wild condors 1982 to 1985.<sup>a</sup>

Bird	Sex	Age (years)	Year	No. of photo dates	Right wing primaries										Left wing primaries										Molt sequence complete <sup>b</sup>					
					3	4	5	6	7	8	9	10	3	4	5	6	7	8	9	10										
SBM	M	Ad.	1982	45	1	2	3					4	5					1				2	3	4	C					
			1983	40	4	1		2	3				3	6					1	2			3	5	4	C				
			1984	45	4	4	1	2	5				3	6					1	2			3	4	5	C				
			1985	68	1	2	2	3					3	4					1	3			2	4	5	C				
SBF	F	Ad.	1982	25	1	2	2	3			3	4						1	2			2	3	4	5	PC				
			1983	33	1	1	2	3					4	4				1	2			2	3	4	5	C				
			1984	34	1	1	2	3					4	4				1	2			2	3	4	5	C				
			1985	58	1	1	2	2	3				4	4				1	2			2	3	4	5	C				
			1982	21	1	1	2	2	3				3	4				1	2			2	2	3	3	4	5	C		
CVM	M	Ad.	1982	21	1	2	2	3			3	4						1	2			2	2	3	4	5	C			
			1983	27	1	1	2	3					4	4				1	2			2	2	3	4	5	C			
			1984	39	6	1	2	2	5				3	4				1	3			1	2	5	3	4	5	C		
			1982	17	1	1	2	2	2				3	4				1	2			2	2	5	3	4	5	C		
CVF	F	Ad.	1982	17	1	1	2	3			3	4						1	2			2	2	3	4	5	C			
			1983	31	1	1	2	2	4				3	4				1	2			2	—	3	3	4	5	C		
			1984	34	1	1	4	—	2				3	5				2	4			1	2	—	3	3	4	5	C	
			1982	26	1	4	3	5					3	5				2	4			1	2	5	3	4	5	C		
PCA	M	Ad.	1983	26	1	4	2	3			3	5						1	2			2	5	3	4	5	C			
			1984	26	1	4	2	5					3	4				1	3			2	4	2	6	4	5	C		
			1985	49	3	1	4	2	2				3	4				1	3			2	7	—	6	4	5	C		
			1982	24	1	1	3	2	3				2	4				1	2			2	3	2	4	3	4	5	C	
PCB	M?	Ad.	1982	24	1	1	3	2	3			4	5					1	2			2	3	2	4	3	4	5	C	
			1983	25	1	3	1	4	2			2	4					5	1			2	4	2	4	3	4	5	C	
			1982	23	1	3	1	2	2				4	4				5	1			2	5	2	4	3	4	5	C	
			1983	27	3	1	1	2	3				2	4				4	1			1	3	4	2	3	4	5	C	
SMM	M	Ad.	1984	25	1	5	2	3			3	4					2	2			1	3	4	3	4	5	C			
			1985	59	1	5	2	3					4	4				2	1			1	3	4	3	4	5	C		
			1982	19	1	1	3	5	1				2	4				4	1			1	3	4	5	2	4	5	PC	
			1983	28	3	1	2	4	5				3	4				4	1			1	3	4	2	5	4	5	C	
CCF	F	Ad.	1984	41	1	2	4	5			3	3					2	3			1	2	3	4	5	6	7	C		
			1982	19	1	2	4.5	3					4.5	6				6	2			1	2	3	4	5	6	7	C	
			1983	17	1	2.5	3	2.5					4	4				—	1			1	3	4	2	3	4	5	6	PI
			1984	27	1	5	3	2					4	6				4	1			3	4	2	4	3	4	5	6	7
CCM	M	Ad.	1985 <sup>c</sup>	62	1.5	1.5	4	5			3	3				1	1				1	2	3	4	5	6	7	C		
			1982	21	1	1	2	2					3	4				2	2			1	2	3	4	5	6	7	C	
			1983	22	1	3	2	2					4	5				2	2			1	2	3	4	5	6	7	C	
			1984	27	1	1	2	2	4				3	4				2	2			1	2	3	4	5	6	7	C	

TABLE 1. Continued.

Bird	Sex	Age (years)	Year	No. of Photo dates	Right wing primaries										Left wing primaries										Molt sequence complete <sup>b</sup>	
					3	4	5	6	7	8	9	10	3	4	5	6	7	8	9	10						
SSM	M	Ad.	1982	19	2	3	1						4					3	1	2	2	4	4	5	PC	
			1983	32	3	4	1	2	6					2					1	3	3	5	4	4	5	C
			1984	24		1	3							2					2		3	5	4	4	4	C
SSF	F	Ad.	1982	17	2	2	1	3	4				3					2	1	2	3	5	3	4	PC	
			1983	32	1	4	2	2	5					3					1	2	4	3	3	5	C	
			1984	21	1	1	2	5	3					4					1	2	4	3	3	4	5	C
			1985	55	1	3	2	5	4					4					1	2	3	4	3	4	5	C
			1982	21	2	2	1	1	4					3					2	1	2	3	3	3	4	5
UN1	F	Ad.	1983	28	1	2	2	3	4	6			4					1	2	6	2	4	4	5	PC	
			1984	16	1	3	2	2	4	6			5					1	3	1	2	2	4	3	C	
			1985 <sup>c</sup>	44	2	2	1	4	3				3					2	1	1	4	1	2	3	4	C
			1983	2		2	2	1						1					2		2	2	1	1	1	PI
SMA	M?	Ad.	1982	3													1							PI		
HIW	M	2	1982	14	2	3	2	3				1						1	3	4	5	2	1	1	PC	
			1983	24	1	4	2	4						3					1	2	5	3	4	3	C	
			1984	13	1	2	1	2	4					3					1.5	1.5	5	4	6	3	C	
			1985 <sup>c</sup>	38	1	2	3	3	3					3					1	2	2	3	3	3	C	
			1982	14	2	1.5	1.5	3	4					6					1	2	1	2	3	5	4	PC
REC	M	3	1983	22	1	2	3	4				5						1	2	3	4	2	4	5	C	
			1984	29	2.5	4	2.5	1	5				6						1	3	1	2	4	5	C	
			1985	82	3	1	2	4						5					3	1	3	4	2	4	5	C
			1982	15	4	1	3	3	4					2					4	1	2	4	3	4	5	PC
			1983	27	1	2	1	3	4					4					1	2	1	2	4	3	4	C
BFE	M	4	1982	15	2	3	4	5				6						1	2	3	4	2	4	5	C	
			1983	27	1	2	1	3	4				2						1	2	4	3	4	5	2	C
			1984	28	6	1	2	4						3					2	4.5	1	3	4	4.5	3	PC
IC1	M	3	1982	7	1.5	3	4	5				5						1	2	3	4	3	4	5	C	
			1983	19	1	3	2	3	4				5						1	2	5	3	4	4	6	C
BOS	F	1	1983	34	1	2	3				2						1	4	3	2				C		
PAX	M	1	1982	17	1												1	4	3	2				C		
WGI	?	1	1982	5	1	2	3										1	2	3					PC		

<sup>a</sup> Sequences given refer to timing of feather loss within birds, years, and wings. Tied feathers given as mean ranks. Dashes represent cases in which feathers dropped late in previous year but were replaced during year in question. One bird photographed in early 1982 disappeared before it commenced primary molt.  
<sup>b</sup> C = Complete, PC = probably complete, PI = probably incomplete.  
<sup>c</sup> Bird brought into captivity during molting season.

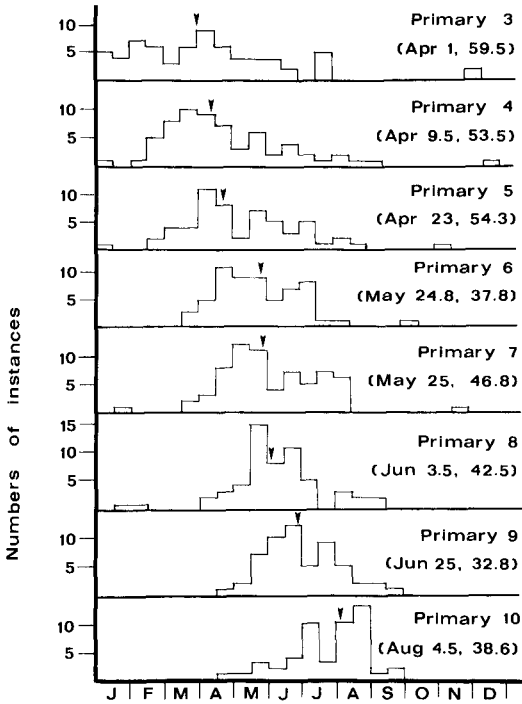


FIGURE 2. Timing of loss of various primaries. For each feather, timing is plotted as the midpoint of the interval between the last time the feather was photographed as still present and the first time it was photographed absent. Arrows indicate median loss dates for the various primaries. Median loss dates are also tabulated along with standard deviations of loss dates.

years (Table 1). Likewise, the pattern exhibited by IC1, another wild bird, in his third and fourth molts was very similar to that of many captives in their first and second years. On the other hand, HIW, another wild bird, showed a very irregular and individual molting sequence in his second year. Although molt of HIW was not followed in his first year, the irregular second-year pattern shown by this bird suggests that his first molt may also have been quite irregular. The only other wild immature for which data exist in the late immature stages was BFE, first studied in his fourth year. The molt of this bird showed some resemblance to that of IC1 and REC in their fourth years, but by his sixth year, BFE's molt (especially his left wing) had become essentially adult in pattern.

In adults, molt was distributed relatively evenly across the span from primary 3 through 10 in any one year, although the exact patterns varied greatly from bird to bird. In some adults there

TABLE 2. Rank orders of primary molt (see Table 1).<sup>a</sup>

Primary no.	No. of instances	Mean rank	SD
3	71	1.52	1.03
4	68	2.02	1.22
5	70	2.20	1.27
6	68	2.75	1.14
7	70	3.22	1.16
8	55	3.31	1.10
9	61	3.61	0.90
10	55	4.47	0.98

<sup>a</sup> Only birds with complete or probably complete molt sequences considered.

was a tendency toward molting every other primary in one season's molt, but in the cases where this pattern was approached most closely, it was not followed consistently through the years nor from one wing to the other.

Usually the primaries molted in one year were not molted the next year and vice versa, so that all primaries tended to molt about once every 2 years. However, primaries sometimes molted twice in 2 years and occasionally failed to molt even once in 2 years. For the 16 primaries numbered 3 through 10, the average for both male and female wild birds was 4.4 primaries molted per wing per year. The average for captives (Table 3) was almost identical at 4.3 primaries per wing per year.

When the same primary molted twice in 2 years, there was a strong tendency for the feather to drop early in the first year and late in the

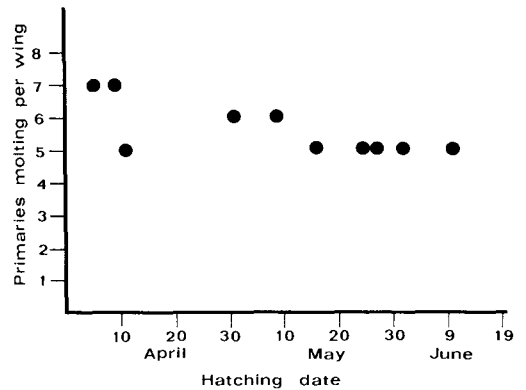


FIGURE 3. Numbers of primaries molted per wing in first molting period as a function of hatching date in previous year. Only birds with accurately known hatching dates are considered.





TABLE 4. Frequency of primary molt of wild California Condors in 2-year periods.<sup>a</sup>

Primary no.	No. of cases primary molts 0 times in 2 years	No. of cases primary molts once in 2 years	No. of cases primary molts twice in 2 years	Mean molting interval	
				Years <sup>b</sup>	n
3	1	57	20	1.64	21
4	0	63	15	1.60	28
5	0	65	13	1.76	26
6	1	67	10	1.74	30
7	1	61	16	1.71	28
8	0	72	6	1.82	21
9	0	76	2	1.93	27
10	3	74	1	2.09	20

<sup>a</sup> Only birds with complete or probably complete molt sequences followed in consecutive years considered.

<sup>b</sup> Calculated as the elapsed time between consecutive drop dates or completion dates for various feathers. To reduce bias, no interval was included in the tabulations if less than 2 years of data was available for the feather in question following the first drop date.

second year. In the first year, such feathers had an average rank of 1.6, whereas the rank average in the second year was 3.6, a highly significant difference ( $z = -7.753$ ,  $P < 0.001$ , Wilcoxon's signed-ranks test). In addition, there was a general trend for low-numbered primaries to be replaced more frequently than high-numbered primaries (Table 4). The average interval measured between consecutive molts was highly significantly correlated with primary number ( $r_s = 0.88$ ,  $P = 0.005$ ) and ranged from 1.60 years for primary 4 to 2.09 years for primary 10.

Thus, the overall pattern was for birds to molt primaries slightly faster than on a 2-year cycle, and this led to discrepancies from a regular alternation of molt and nonmolt years for individual primaries. If discrepancies are defined as cases where a primary molted twice in 2 years or not at all in 2 years, it is straightforward to examine the numbers of discrepancies per bird in year to year comparisons. The average number of discrepancies within individuals was 1.8 (range 0 to 4) between 1982 and 1983, 2.4 (range 0 to 5) between 1983 and 1984, and 2.8 (range 0 to 5) between 1984 and 1985. The overall average was 2.2 (range 0 to 5). For each bird, discrepancies were fewer, or at least no greater, with itself than with other individuals, and the overall distribution of between-individual discrepancies (Fig. 4) suggests that it is unusual to have three or fewer discrepancies (only 2.4% of the total comparisons). On the average, there were 8.0 discrepancies between individuals, and the between-individual distribution is highly signifi-

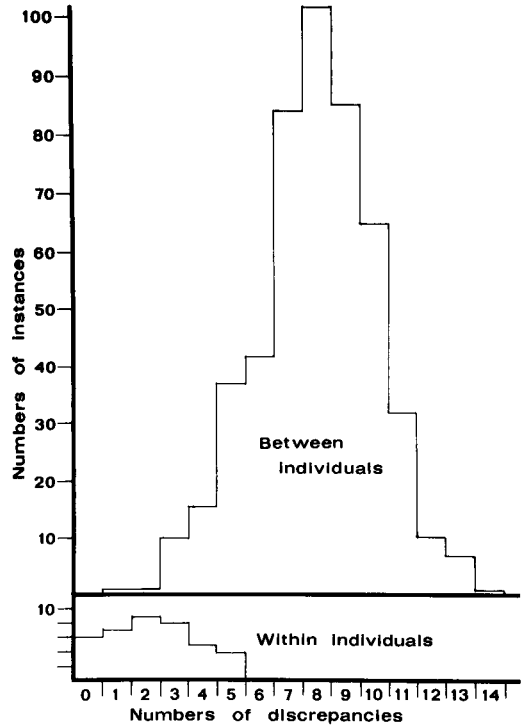


FIGURE 4. Distribution of numbers of primary feather discrepancies between and within individuals in consecutive years (1982 to 1985). Discrepancies defined as feathers molting twice in 2 years or not at all in 2 years.

cantly different from the within-individual distribution by a median test ( $\chi^2 = 41.92$ ,  $P < 0.005$ ).

Thus, identification of individuals from year to year can be determined quite reliably by matching birds with the fewest discrepancies. This conclusion is not circular, because essentially all birds studied have also been identifiable from year to year by means other than feather discrepancies—most importantly by peculiarities of feather damage, but also by other information such as patagial tags on some birds, head color characteristics in some birds, and behavioral peculiarities, especially traditional use of certain nesting and roosting areas. The only individuals for which we were forced to rely entirely on discrepancies in year to year identifications were UNI and BFE for 1983 to 1984.

It is also possible to compare the molt pattern of one wing of a bird with that of the other wing in the same year, defining discrepancies as feathers that molt on one wing and not on the other (Table 5). Right-left discrepancies tended to be

TABLE 5. Between-wing primary feather discrepancies within individuals from 1982 through 1985.<sup>a</sup>

Bird	Age (years)	No. of discrepancies			
		1982	1983	1984	1985
SBM	Ad.	3	1	3	3
SBF	Ad.	5	5	5	5
CVM	Ad.	5	7	6	—
CVF	Ad.	6	5	6	—
PCA	Ad.	5	5	4	3
PCB	Ad.	4	4	—	—
SMM	Ad.	0	1	1	1
PPF	Ad.	2	3	3	—
CCF	Ad.	0	—	2	1
CCM	Ad.	3	3	2	—
SSM	Ad.	2	1	2	—
SSF	Ad.	2	2	2	3
UNI	Ad.	3	2	2	0
HIW	2-5	2	3	4	4
REC	2-5	1	0	1	2
BFE	4-6	2	3	3	—
ICI	3-4	1	1	—	—
BOS	1	—	1	—	—
Mean change between years		0.0	+0.2	-0.2	

<sup>a</sup> Feather discrepancies defined as feathers molting on one wing but not the other. Only birds with complete or probably complete molt sequences considered.

fewer among immatures than among adults, but this tendency did not reach statistical significance by a median test ( $\chi^2 = 2.04, P > 0.10$ ). Among adults, the average number of right-left discrepancies within individuals (3.1) was reasonably close to the average number between individuals (3.9), suggesting a high degree of independence of molt between wings. Whether the adults showing the most right-left discrepancies were the oldest individuals is unknown. In the four years covered in Table 5, there was no overall trend toward increasing numbers of between-wing discrepancies in individuals from one year to the next.

RATES OF PRIMARY GROWTH

In Figure 5 we present the distributions of minimum and maximum replacement intervals for the various primaries in the zone where these values converge (approximately 100 to 125 days). In general, the rates of feather growth seen for the various primaries were quite uniform among different individuals in the population, judging from the small amount of overlap in maximum and minimum periods for most primaries. Average molt period, defined for each primary as the mean of the 10 smallest maximum periods

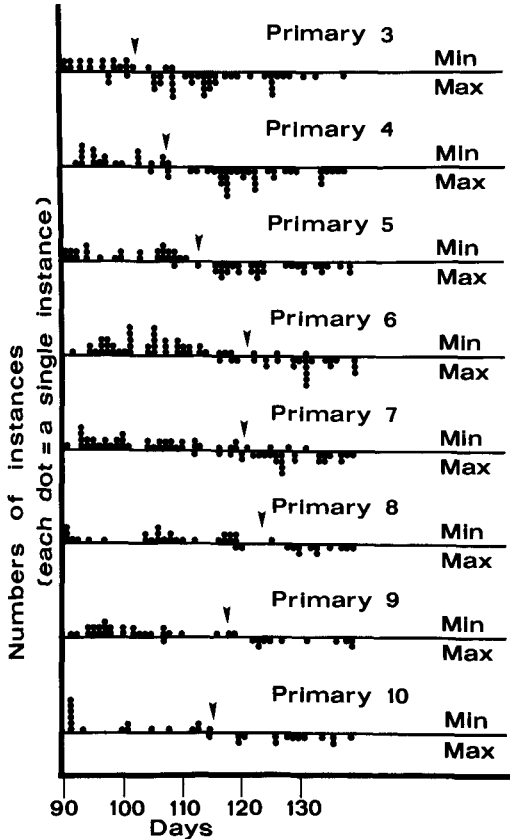


FIGURE 5. Minimum (above axis) and maximum (below axis) periods from loss to full replacement for given primaries. Arrows delineate average replacement periods, computed as means of the 10 highest minimum values and 10 lowest maximum values for each primary.

and 10 largest minimum periods, ranged from about 3½ to 4 months and varied systematically with primary number. There was a bias toward lengthy loss-replacement periods for the primaries closest to the leading edge of the wing. A comparison of average period lengths with actual feather lengths of two representative individuals and with feather weights of primaries collected below roosts over the years (Fig. 6) shows that, while primary 10 is the shortest primary in length and lightest in weight, its average loss-replacement period is longer than those of primaries 3, 4, and 5. Why primaries at the leading edge of the wing have relatively sluggish replacement periods is unknown, but this appears to be a regular feature of molt in other families of birds as well (e.g., Newton 1967, 1969).

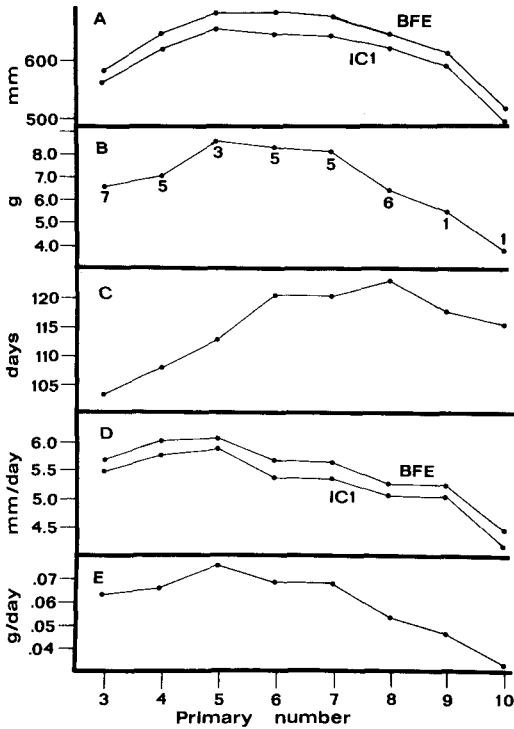


FIGURE 6. A. Measured total primary feather lengths for two birds: BFE, an adult (Los Angeles County Museum 102739), and ICI, a subadult (LACM 101811). B. Average weights of primaries (sample size given for each). C. Estimated average loss-replacement periods for various primaries from Figure 5. D. Calculated growth rates for various primaries based on A. and C. E. Average growth rates for various primaries based on B. and C.

SEASONAL TIMING OF PRIMARY MOLT AND INTERRUPTED OVERWINTER MOLT

Most primaries were shed between 1 February and 1 September (Fig. 2). Since primaries shed at the end of this period tended to be the higher-numbered primaries and took close to 4 months to replace, birds were commonly in some state of primary molt (either with missing or partly

grown primaries) up to 9 or 10 (occasionally 11) months out of the year. Individuals were most likely to show no evidence of molt from November through February.

In addition to the steady seasonal progression of median drop dates for individual primaries (Fig. 2) there was a significant reduction in variance of drop dates as one moves up the primary sequence ( $r_s = -0.79, P < 0.025$ ). Thus primaries 3 and 4 were quite likely to drop at any time during the molting season, while primaries 9 and 10 were quite consistently shed in the latter part. At least in part, this reduction in variance is a reflection of the progressive reduction in the tendency for primaries to molt in consecutive years as one moves up the primary sequence (Table 4), as consecutive-year molting of primaries normally entails early molt in one year and late molt in the next.

Mundy (1982) found a marked depression in molting activity of older (presumably breeding) accipitrid vultures in Africa during the breeding season. In adult condors there was likewise a difference in the seasonal timing of molt between breeding and nonbreeding birds (Fig. 7). Breeders of both sexes showed a clear tendency to begin primary molt earlier and end it later than non-breeders, presumably leading to a relatively greater retention of flying abilities for breeders during the middle portion of the breeding season.

The occasional feathers lost in late fall or early winter had exceptionally long periods for replacement, indicating a period of interrupted molt over the winter (Table 6). We excluded these feathers from the general calculations of rates of feather replacement (Fig. 5) because of their obviously exceptional nature. In all of these cases a protracted period of no-growth occurred prior to the initiation of visible growth of replacement feathers, and the birds exhibited feather gaps in their wings lasting in some cases over half a year. For unknown reasons, all instances of long-lasting gaps involved primaries 5 through 7. There

TABLE 6. Cases of interrupted primary molt over the winter.

Bird	Primary	Date last present	Date first missing	Date last short	Date first complete	Minimum period (days)	Maximum period (days)
CCF	L-5	11-2-82	11-24-82	5-27-83	6-13-83	184	223
PCA	R-6	—	11-25-81	6-23-82	7-31-82	210	—
PCA	L-6	—	11-25-81	6-23-82	7-31-82	210	—
PCA	L-6	9-23-84	10-22-84	7-30-85	8-5-85	281	316
CVF	L-7	10-27-82	12-26-82	5-29-83	6-30-83	154	246

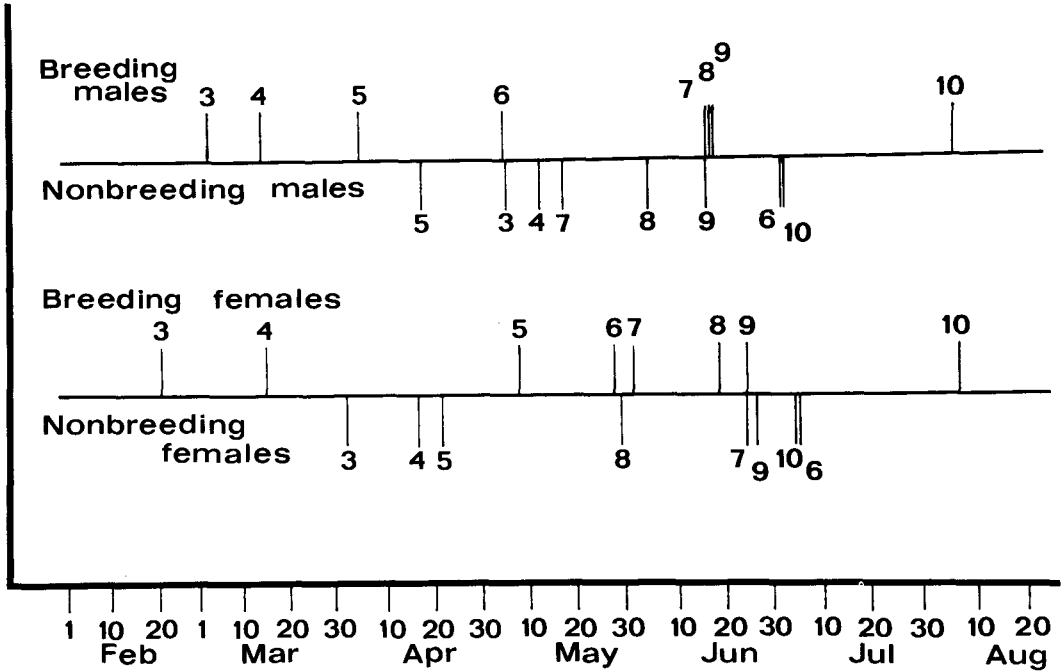


FIGURE 7. Median drop dates for primaries of breeding and nonbreeding adult California Condors. Primary number given for each median date.

were no indications that these cases might have involved feathers accidentally breaking off near their bases prior to molt.

MOLT OF SECONDARIES AND RECTRICES

In their 2-year molt study of Topatopa, a captive bird obtained before its first molt, Todd and Gale (1970) reported no tail molt and essentially no secondary molt in the first molting period, then complete and almost complete molt of these feather categories in the following year. While the photographic method was not adequate to give detailed information on molt of these feathers in wild birds, it was informative enough to confirm much of what Todd and Gale reported. Although we saw limited signs of molt of rectrices and secondaries in some wild yearlings, the generally smooth contours of these feathers in photographs of yearlings suggested minimal molting as a rule.

However, a yearling female (BOS) that died and was recovered shortly after completing her first molt in November 1983, had replaced 4 of her 12 rectrices (L1, L2, R1, and R3) and 3 of 22 secondaries on each wing (L1, L19, and L22; R1, R15 or R16, and R21) (see Fig. 1B). Topatopa molted his L11 and R17 secondaries (pos-

sibly also his R9 and R16 secondaries) in his first molting period, a completely different pattern. Furthermore, when tail molt commenced in Topatopa in his second molting period, the order of replacement of rectrices (L4-L5, L3, L6, L2, and L1; and R1, R6, R4, R2, R5, and R3) was quite different from that of BOS.

Tail molt among recently-hatched captives generally followed a pattern of no replacements in the first year (seven birds examined in 1985), followed by partial replacements in the second year (six birds examined in 1985). The most common patterns in the second molting period were replacement of two outer and two central rectrices (two individuals) and replacement of two outer and four central rectrices (two individuals). One bird replaced two outer and six central rectrices and one molted 2, 3, and 6 on the right side and 1, 2, and 6 on the left, possibly having molted R1 in its first year.

Secondary molt of recently-hatched captives resembled the pattern exhibited by BOS, with all birds examined in the first year (seven individuals) molting secondary 1 on each side, some birds also molting secondary 2 on each side (two individuals), and all birds molting a high-numbered secondary or two close to the body on both

sides (mainly secondary 21 or 22). Secondary molt of the second year was much more extensive, generally involving about half of the secondaries, and was extremely variable in detail but with a general tendency for most replacements to occur near the body and among the most distal secondaries. Molt in the second year did not result in replacement of all original secondaries in the birds checked closely (except Topatopa). Thus as a general rule, a large fraction of the original rectrices and secondaries lasted without replacement into the third molting period (at least in captives). In contrast, essentially none of the original primaries lasted this long, although Cuyama apparently failed to molt primaries 9 and 10 on the left wing in his first two molts, and Cachuma apparently failed to molt primary 10 on the right wing during her first two molts (Table 3).

## DISCUSSION

Among wild individuals, the most deviant molting patterns were found in PCA and PAX. PCA (Fig. 1C) exhibited a consistent tendency to molt more primary feathers than average and in one year (1985) actually replaced every primary from 3 through 10 on his left wing (although one of these primaries had dropped late in 1984). PCA also consistently exhibited the highest number of primary feather discrepancies of any wild bird from year to year. In addition, PCA accounted for more than half the instances documented in the wild population of birds dropping primaries in the fall and not replacing them until the following summer. Remarkably, every such case with PCA involved a primary 6. No causes for these peculiarities are known.

PAX in 1982 represented another extreme, replacing only a single primary of the 16 possible between numbers 3 and 10 on his two wings. PAX's molt also started very late in 1982 (late July), and it is possible that this bird fledged extremely late in 1981 or possibly even early in 1982. However, the extremely abbreviated molt of PAX in 1982 might alternatively have been related to poor health or genetic problems. When this bird was trapped for the captive flock in late 1982, it was quite light in weight and gaped with the slightest exertion. Chronic gaping is a trait PAX has retained as a captive to this day.

Among captives, the most unusual molt was exhibited by Topatopa, who showed a strong tendency to finish molting his first primaries through

primary 10 before starting another molt wave of low-numbered primaries. Topatopa was also unusual in molting all tail feathers and nearly all secondaries in his second year. We are unable to account for these peculiarities.

In general, however, the patterns of molt documented in wild and captive juvenile condors were quite similar, suggesting that captivity was not producing great distortions in molting patterns. The numbers of primaries molted per year, the sequences followed, and the seasonal timing of molt all appeared to reflect the same general patterns, although there was considerable variability in detail in both wild and captive individuals. The clearest effect of captivity on molt was seen in HIW, UNI, and CCF, all of whom were captured in the midst of the molting season in 1985, and all of whom exhibited some primary feathers that did not quite reach full length, apparently as a result of the stress of capture and adjustment to captivity during the period of growth of these feathers. The failures of HIW to molt primary R10 and of UNI to molt primary L10 in 1985 could also have been a result of capture.

Although Miller (1937) reported a California Condor specimen with 13, rather than 12 rectrices, none of the wild or captive condors observed in this study, so far as could be determined, exhibited unusual numbers of flight feathers. Mundy (1982) found low frequencies of individuals (generally about 5%) with more or fewer primaries and rectrices than normal in five species of African vultures.

## SEASONAL CONSIDERATIONS

The seasonal timing of primary molt documented in this study (mainly March to October) matches that reported for condors by Wilbur (1975). Wild California Condors most commonly lay eggs in February or March, hatch eggs in April or May, and fledge young in September or October. Young remain strongly dependent on their parents until the following spring, and adults commonly do not breed in years following successful fledging of young (Koford 1953, Snyder and Hamber 1985). Thus, primary molt in the species normally coincides with the egg-nestling-early fledgling phases of the breeding cycle, and the period of heaviest molt—midsummer—is the season of heaviest food demands in reproduction, a period that is commonly avoided in molt of other avian species (Payne 1972). How-

ever, for the condor it appears that summer is also a period of reasonably good food availability and consistently good foraging weather (Miller et al. 1965).

Thus, the seasonal timing of molt in condors may relate more to foraging opportunities than to the reproductive cycle per se. The winter months, December through March, are normally the period of most frequent storm fronts in southern California, while from May through October it is unusual to see much, if any, rainfall. During periods of heavy rainfall and low clouds, condors are unable to forage efficiently, and their opportunities for finding food are often limited to brief 1- or 2-day windows of good weather between successive fronts. In addition, the relatively short daylengths in the winter months automatically reduce the potential hours for foraging to a significant extent (see Johnson et al. 1983). Further, food needs in winter are relatively high because of low temperatures, yet periods of cold weather can inhibit feeding by freezing carcasses, making them difficult for condors to ingest. Thus, it may be critical that the birds are in their most perfect plumage in winter so they can move about the foraging grounds with maximal efficiency.

While the abilities of condors to survive starvation are undoubtedly well developed (we have seen incubating birds sit as long as 10 days without food), the capacities of the birds to attain good physical condition for the initiation of reproduction may depend on their abilities to cope with limited foraging opportunities in winter and on their avoidance of the metabolic costs of molt during this period. Furthermore, molt attempted during periods of food deprivation in winter may pose risks of the production of short or structurally weak feathers. The fact that molt normally begins in the spring with low-numbered primaries, while high-numbered primaries, possibly more critical to flight, are not shed until the dry midsummer period, may minimize the penalties of starting molt before the winter and spring storms are over.

The near absence of molt in secondaries and rectrices, and the restriction of molt to low-numbered primaries in yearlings is of special interest. Because yearlings probably face the greatest mortality rates of any age-class of free-flying condors as they develop abilities to forage on their own and compete for food at carcasses, it seems reasonable that these birds restrict molt greatly, in

the sense both of avoiding metabolic costs of molt and avoiding the penalties resulting from reduction of effective wing surface area. However, the delays in completing first molt of rectrices and secondaries result in some of these feathers being in service for 3 years, which poses risks of excessive feather wear for parts of the flight surface during the third year.

#### COMPARISONS WITH OTHER SPECIES

Various features of primary molt of California Condors find instructive parallels and contrasts in the molt of large accipitrid vultures in Africa. Mundy (1982) noted that all five species he studied in southern Africa greatly reduced molt during the winter months, a pattern similar to that of *Gymnogyps*. However, unlike the situation with *Gymnogyps*, the winter months for these species are the dry season and are the central part of the breeding season, when the birds are tending eggs and nestlings. This correspondence in season, but not in weather or in stages of the breeding cycle, might be taken as evidence that the primary factor controlling timing of molt in large vultures is daylength, perhaps through its influence on foraging opportunities. Apparently consistent with this possibility is the fact that Houston (1975) was unable to find much evidence for seasonal change in molt of *Gyps africanus* and *G. rueppellii* in an equatorial region of central Africa with relatively uniform daylength throughout the year. However, Mundy (1982) provided an alternative explanation for relatively nonseasonal molt in this region, based on relatively low seasonality in weather conditions.

The data of Mundy and Houston indicate that juveniles of the African species, like those of the California Condor, begin first molt of primaries about 8 to 9 months after fledging and that primary molt of juveniles proceeds quite regularly up the sequence. Very little secondary or tail molt was seen until about a year and a half after fledging, also corresponding to the situation in *Gymnogyps*. Further, although the data of these authors do not cover molting patterns and sequences of adults in detail, their data for young birds suggest that primary feathers may molt on a greater than 1-year cycle, as in *Gymnogyps*. Commonly in these species, a second wave of molt started up the primary sequence before the first wave carried through the higher-numbered primaries, again similar to *Gymnogyps*.

By repeated measurements of growing primary

and secondary feathers of captive *G. africanus*, Houston (1975) calculated a very uniform rate of feather elongation of 4.4 mm per day. Similarly, Mundy (1982) found that primary growth of nestling *G. africanus* proceeded at 4.7 mm per day. While we have not made the same sorts of measurements for *Gymnogyps*, we know the lengths of the total periods from loss to full replacement of the various primaries with some accuracy and calculate that averaged over the entire period, rates of elongation for the various primaries range from 4.3 to 6.0 mm per day (Fig. 6). While growth of *Gymnogyps*' primaries appears to average somewhat faster than that of *G. africanus*, primaries of *G. africanus* are somewhat shorter than those of *Gymnogyps*, and Houston's estimated times for replacement of the various primaries of this species (95 to 124 days) are strikingly similar to the replacement periods documented in this study.

Although the replacement periods for individual primaries may be quite similar in the two species, it appears that the numbers of primaries in molt at the same time vary considerably, with the fewest number molting simultaneously in the equatorial *G. africanus* studied by Houston (1975), considerably greater numbers found during the main molting season of *G. africanus* in more southerly regions of Africa (Mundy 1982), and even more primaries molting simultaneously at the height of the molting season of *Gymnogyps*. Houston rarely found more than two primaries simultaneously in molt for juveniles or more than four primaries simultaneously in molt for older birds, and he emphasized that primaries were characteristically not shed until the preceding primaries in sequence were fully grown. Mundy found an average of 3.7 primaries simultaneously in molt for juveniles and 4.3 primaries simultaneously in molt for adults during the season of heaviest molt (October through December). In *Gymnogyps*, from July through September and considering only primaries 3 through 10, the average number of primaries in molt simultaneously for all birds was 5.1 (4.6 for immatures and 5.3 for adults). Correspondingly, the period of molt appears to be most seasonally concentrated for *Gymnogyps*, less so for *G. africanus* in southern Africa, and apparently least so for *G. africanus* in equatorial Africa. During the heavy molt period of *Gymnogyps*, individuals sometimes have fewer than four of the emarginated primaries on a wing fully operational (Fig. 1C),

and it seems likely that such individuals suffer considerable losses in flying abilities.

Prevost (1983) suggested that there seem to be limits to how fast developing flight feathers can elongate, basing this conclusion on a review of literature on feather growth in many different groups of birds. A number of authors have argued that the extended lengths of time it takes to grow the long primaries in large flying birds in effect force these birds into a molt dilemma (Stresemann and Stresemann 1960, 1966; Stresemann 1963, 1967; Edelstam 1984). Either they cannot replace the feathers frequently (e.g., annually) or they must replace them to a greater or lesser extent on a simultaneous basis. However, if a number of primaries are in molt simultaneously, it becomes disadvantageous to molt them in the simple sequential order characteristic of most small birds because large gaps would form in the airfoil.

As discussed by the above authors, a number of apparent solutions to the above problem have evolved in different groups of relatively large birds. For example, falcons and parrots molt primaries in two directions simultaneously from a central focus. Some cuckoos follow a pattern of molting every other primary in sequence, then molting the ones missed in a second round through the sequence. Many large accipitrids and other groups follow a pattern that has been termed a serial molt or "Staffelmauser" in which primaries molt in a sequential order but in which new waves of molt begin before old ones have finished. In young birds these waves tend to be far apart in the primary span, but in older birds several molt waves may be proceeding up the primary sequence simultaneously in roughly parallel fashion. Edelstam (1984) claimed that the Staffelmauser pattern of molting is characteristic of all large cathartids, and it has also been reported in their close relatives, the storks, by Bloesch et al. (1977). Edelstam also commented, however, that as individuals of the largest species age, inconsistencies appear that disturb the pattern, and in "adult large vultures it may be difficult occasionally to trace any organized molting pattern at all," a conclusion earlier advanced by Stresemann and Stresemann (1960).

With the California Condor, it is possible to interpret many of the molt patterns in Tables 1 and 3, especially those of young birds, as being consistent with a Staffelmauser arrangement. However, a close examination of the data indi-

cates fairly frequent distortions of the pattern, especially in older birds, and it is questionable how useful it is to describe the molt pattern of adults as a series of roughly parallel waves moving up the sequence. For one thing, the waves one can trace in Table 1 are exceedingly variable in speed, sometimes covering a 3-primary span (or more) in one year and sometimes taking 3 years to go the same distance. Such variability can sometimes be seen in different parts of the same wing of the same bird in the same years (e.g., SBM's right wing from 1982 to 1984). Moreover, waves appear to catch up with each other and die out on occasion. For example, two molt waves in SBM's left wing in 1982—positioned at primaries 5 and 7—end up being a single wave by 1984—primary 9, and then 10. And on occasion, waves appear to originate in the middle of the primary span without any antecedents (e.g., a wave starting at HIW's left primary 7 in 1984). In itself, the Staffelmauser concept does not explain why primary molt in condors has a strong tendency to begin close to the low end of the sequence and end close to the high end of the sequence each year (although this pattern is not necessarily inconsistent with the Staffelmauser concept).

Instead of describing molt of adult condors as a series of roughly parallel waves, one could alternatively describe it as a pattern in which about half of the primaries molt each year, and although these can be almost any combination of specific primaries, molt tends to move roughly as a single wave up the sequence, replacing feathers that had not molted in 2 years and skipping feathers that molted the previous year, or at least late in the previous year. More specifically, feathers that are not molted in one year are almost always molted in order up the sequence the next year, although in the second year, birds also often molt one or two feathers that molted early in the previous year. These repeats tend to come late in the molting period of the second year, but often occur intermixed in sequence with molt of feathers that did not molt in the first year. The overall validity of this description is clear from Tables 1 and 2 and Figure 2.

As another alternative, it might be best not to talk about molt waves at all but instead to describe molt order as simply a consequence of different seasonal specificities of various primaries in timing of molt potential (Fig. 2) in interaction with a periodic factor driving feather

replacement at rough intervals of 2 years (Table 4). An apparent molt wave could be a result of factors such as these, rather than itself being a "driving force" in determining the order in which primaries are replaced.

In contrast to the complicated patterns of primary molt characteristic of adult California Condors, wing molt of the smaller cathartids appears to be quite simple. Regular sequential molt of primaries has been especially well studied in captive and wild Turkey and Black vultures (*Cathartes aura* and *Coragyps atratus*) by Amadeo Rea (unpubl.). In these species, primaries are replaced in an almost invariant 1 through 10 sequence, regardless of age of the bird, although new molt cycles generally start in late summer before preceding cycles are completely finished, so that both low- and high-numbered primaries are commonly missing or growing simultaneously at this time. Both *C. aura* and *C. atratus* replace all primaries on an annual basis, and despite the fact that both species occur in highly seasonal environments and breed on a highly seasonal basis in North America (Jackson 1983), molt in both species is spread throughout the year so there is no period of true molt arrest in one season.

Perhaps the most detailed published study of flight feather molt of a large soaring species has been that of Bloesch et al. (1977) on the White Stork (*Ciconia ciconia*), and it is informative to compare their results with our own because of the well-documented close taxonomic relationship of storks with cathartids (see Rea 1983, Sibley and Ahlquist 1986). Like the California Condor, the White Stork molts about 55% of its primaries each year, and although this species has 11 functional primaries while the condor has only 10 (primary 11 is vestigial in cathartids), other aspects of molt in these two species are also quite similar. In both, low-numbered primaries are replaced more frequently than high-numbered primaries. In the stork, average periodicities range from once every 1.2 years for primary 1 to once every 2.5 years for primary 11, values very similar to those for the condor given in Table 4. Further, in both species growth rates of the various primaries show a peak at about primaries 5 and 6, with especially slow growth of the outermost primaries (10 or 11). In addition, the seasonal timing of molt is very similar (spring to early fall) in both species, and coincides with the breeding season for both species.



Principal differences in molt between the species lie in the regularity of secondary molt and in the rigor with which they approach a Staffellauser molt pattern overall. Bloesch et al. (1977) documented a quite consistent pattern of secondary molt starting with three foci—secondaries 1, 5, and 21 or 22—and presented data indicating considerable secondary molt in the first molting period of most individuals. In the captive condors we have examined closely, there has been a fairly consistent pattern for secondary molt to start with secondary 1 and either 21 or 22, but we have seen no sign of a focus at secondary 5 (although Rea [1983] reported such a focus for Black and Turkey vultures). Instead, captive condors have exhibited a variable situation, with several internal foci developing in unpredictable positions in the secondary span after initial molting of the most proximal and most distal secondaries, a pattern very similar to that reported for several species of African vultures by Mundy (1982), and to that reported for the Eurasian Sparrowhawk (*Accipiter nisus*) by Newton and Marquiss (1982). Furthermore, unlike storks, condors do not commonly molt more than secondaries 1 and 2 and one or two feathers in the region of secondaries 19 through 22 in the first molting period.

In general, the molt sequences of several captive juvenile storks (Bloesch et al. 1977) appeared to be much closer to an ideal Staffellauser pattern than we have found in the condor, although these authors too found some irregularities that were difficult to rationalize on the basis of a strict Staffellauser.

Thus, although flight feather molt of the White Stork shows many similarities to the molt of the California Condor and this could be considered to provide further support for a close taxonomic relationship between storks and cathartids, molt of the condor appears to be more similar to that of some large accipitrids in certain respects.

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