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# FLIGHT FEATHER MOLT OF TURKEY VULTURES

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ABSTRACT.—We document the molt sequence of flight feathers in Turkey Vultures (*Cathartes aura*) based on studies of captive and wild birds, and examination of museum specimens. We found an unusual pattern of primary replacement, which appears to be a modified form of *Staffelmauser*, or stepwise wing molt. A *Staffelmauser*-like strategy for replacement of the secondaries is also described. These patterns of feather replacement appear to be adaptations to maintain flying performance while replacing all primaries and most secondaries during each molt. To what extent molt patterns in Turkey Vultures reflect convergent adaptation for flight, rather than ancestral characters useful for phylogenetic studies, remains unknown. *Received 15 June 2009. Accepted 12 January 2010.*

Maintaining optimal flight performance is essential for Turkey Vultures (*Cathartes aura*), a species adapted for long-term soaring (Rosser and George 1986, Tucker 1987). This species locates its primary diet of carrion by detecting odor plumes while aloft, and spends most daylight hours searching for food (Owre and Northington 1961, Stager 1964). It is a migratory species that can travel hundreds or thousands of kilometers seasonally between southern wintering and northern breeding areas (Stewart 1977, Kirk and Houston 1995, Bildstein and Zalles 2001).

Little is known about the molt of Turkey Vultures despite its widespread distribution and abundance (Kirk and Mossman 1998). Identifying and understanding molt processes in birds can be accomplished in several ways. Miller (1941), Stresemann (1963), and Pyle (2005) used data from museum study skins of raptors to make their basic molt sequence hypotheses. Analyzing molt patterns from study skins can be difficult and may not represent the progression of a single individual, and sample sizes of large birds are typically too low to undertake comprehensive analyses. Houston (1975) observed flight feather replacement in both captive and wild individuals of Old World vultures (*Gyps*), but molt in captive birds may not reflect that of wild birds (*cf*. Pyle 2005). Snyder et al. (1987) based their molt study of California Condors (*Gymnogyps californianus*) on photographs of wild birds in flight. Bloom and Clark (2001) used banding records with some recaptures to study the molt of the Golden Eagle (*Aquila chrysaetos*), but sample sizes of known individual birds are low in these studies. Ideally, a complete understanding of molt strategies would be based on the study of wild birds, captive individuals, and specimens; we present such an analysis of molt in Turkey Vultures.

## METHODS

A. M. Rea began collecting molt sequence data on Turkey Vultures in 1972 as part of a larger study on the phylogenetic relationship of New World vultures (Rea 1983). Chandler joined the project in 1978, collecting feathers from three adult individuals held captive at the San Diego Natural History Museum (SDNHM) in San Diego, California, USA and studying molt year-round on several others. Flannery and Long tabulated molt data on five vultures (4 adults and 1first year bird) between 2002 and 2004, which were held captive by the California Academy of Sciences (CAS) in San Francisco, California. The extended study period of captive individuals allows calculation of feather replacement rates both within and between individuals to establish ranges of variation. Pyle and Howell visually examined hundreds of vultures in the field, and Pyle and Flannery examined molt in over 20 museum specimens.

We classified ages of Turkey Vultures using head and bill coloration (Henckel 1981), and known history for captive individuals. Age coding of birds follows Pyle (1997): HY (hatching or first calendar year), SY (second calendar year), TY (third calendar year), and ASY (at least third

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calendar year). Chandler collected data from two captive (SDNHM) ASYs during 1972–1980 and a third ASY during 1979–1980. Flannery and Long collected data from four captive ASYs (3 males and 1 female known to be ages 7+ to 25+ years) and a female received as an HY, housed at CAS during 2002–2004. The ASYs were from Oklahoma, Pennsylvania, and Texas; the HY, received with down still present on the head and the majority of the beak still dark, was from Tennessee and arrived in December 2001. All eight individuals were kept in outdoor pens, ensuring they were acclimated to the natural local photoperiod and climate.

Primaries, secondaries, and rectrices for the vultures studied by Chandler (SDNHM) were painted with a dot and slash code to identify the specific feather (a dot = 1 and a slash = 5), and with a year-specific color for each individual for each year of study. The aviary was checked several times daily for dropped feathers, which were labeled and dated. Wings were examined visually for the individuals at CAS, and dropped feathers were examined to tabulate wing molt data. Primaries and secondaries on each healthy wing of each individual were scored as old, missing, in pin, growing, or new. The percentage of feather length grown was recorded for each growing feather. Data were collected weekly during the first year of the study and biweekly or monthly in subsequent years. Drop dates for each primary on each bird were estimated by calculating primary-specific growth rates and obtaining mean, back-calculated dates for each feather. Feathers not dropped that year were designated as being retained in both studies.

Pyle and Howell recorded data from 1998 to 2006 on wing molt from Turkey Vultures in the field. Binoculars were used to score primaries as missing, growing, new, or old. Molt was assumed if the same primary was missing or growing on both wings simultaneously; individuals with a missing or growing primary on only one wing were not included in the data set. Data were collected year-round and, although most data were obtained from central California, at least 10 birds each from Maryland, Indiana, Mexico, and El Salvador were scored. Vultures observed with dark heads and bills, and no primary molt in June-December were classified as HYs and not included in the data set. Analysis was based on date of observation and progression of molt, including either no molt, or a score representing the number of the primary that was growing on the observation date. Individuals with two primaries being replaced simultaneously from different parts of the wing (e.g., an inner and an outer primary) were scored twice in the data set. Secondary molt patterns also were scored when visible. We analyzed the data using a two-tailed *t*-test with JMP Version 5.1 statistical software (SAS Institute 2002) to examine whether or not there was a difference in mean dates of molt between captive and wild birds.

More than 20 specimens at CAS, Museum of Vertebrate Zoology (MVZ), SDNHM, and the National Museum of Natural History (USNM) were examined. Primaries and secondaries were scored in the same manner as captive birds, and replacement sequences were inferred based on wear clines reflecting protracted molts (Pyle 2005).

## RESULTS

*Primaries.*—All data indicate the 10 primaries of a Turkey Vulture molt sequentially from the innermost primary (P1) to the outermost primary (P10). This process started for the SY at CAS in late January with P1 and was completed in late July with P10 (Fig. 1). This SY then replaced P1–P3 for a second time within the year in September–November (Fig. 1). The following year, as a TY, this individual continued the sequence where it had suspended the year before, replacing P4–P10 in order between early March and early August, and replacing P1–P3 in August–September (Fig. 1). The captive ASYs at both locations replaced P5–P10 in March–September and replaced P1–P2 in July–August (Fig. 1). This pattern averaged later than the drop dates recorded for the younger bird as an SY and a TY. Replacement of P3 and P4 in ASYs was more variable (Fig. 1).

Based on the above results, data on P1–P4 from birds in the field were partitioned as either molting in August–November or in January–March (Fig. 2). The remaining primaries, P5–P10 had sequential mean dates of molt, beginning in April–May (P5) and finishing in September–October (P10). This pattern was similar to that recorded for captive birds of all ages (Fig. 2). Mean dates of molt for P1–P4 and P7–P8 were not significantly different between captive and wild birds. However, mean drop dates were significantly earlier (2-tailed *t*-test, $P < 0.01$) in captive

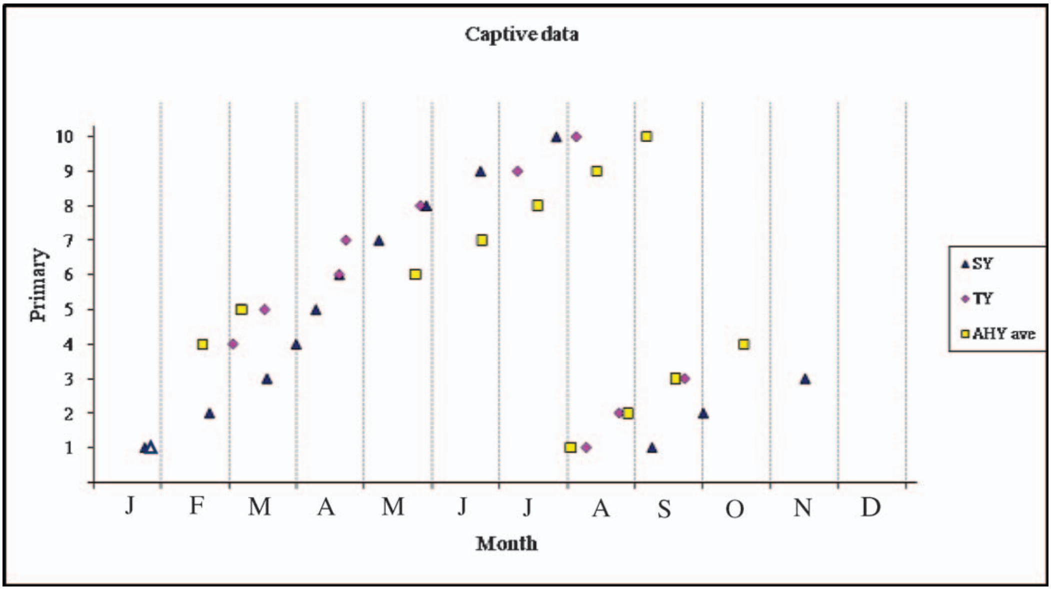

FIG. 1. Calculated feather drop date by month for Turkey Vultures. Data collected from Turkey Vultures held captive at the California Academy of Sciences. SY and TY data collected from same individual during 2002 and 2003. Open triangle represents assumed drop date for P1 in a SY calculated using percentage feather grown, actual drop date occurred prior to acquisition of the bird.

than in wild populations for P5, P6, P9, and P10. This difference is most likely attributable to the higher energy requirements for breeding and food acquisition observed in wild populations that could suspend, slow down, or otherwise delay molt.

Three vultures observed in the field were replacing P1 during 20–29 January. All three

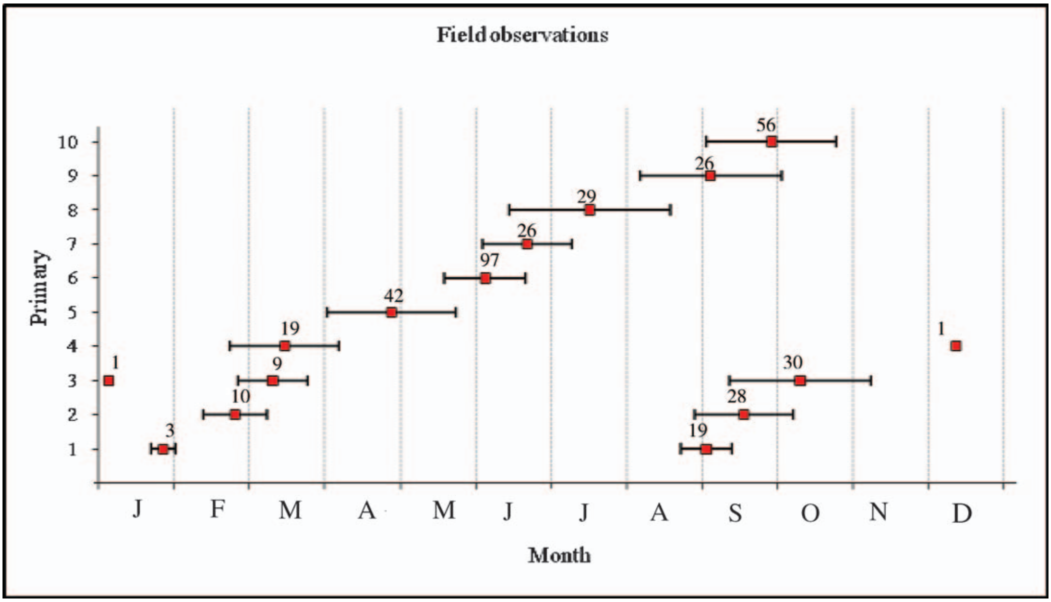

FIG. 2. Mean (± SE) feather drop date for Turkey Vultures by month based on field observations.

were classified as SYs by head plumage and evenly worn primaries (P2–P10). Most of 19 vultures observed replacing P2–P3 in February and March (Fig. 2) were classified as SYs. In contrast, many of the 77 vultures observed replacing P1–P3 in August–November (Fig. 2) were ASYs. Vultures replacing P4 in February–April ($n = 19$) included three SYs and seven ASYs. Two vultures that could not be partitioned into our defined categories were replacing P3 on 4 January and P4 on 7 December (Fig. 2). Both of these individuals were observed in central California. ASY vultures showing no primary molt ($n = 181$) were observed between 6 September and 17 March. The mean (± SD) date for individuals showing no molt was 14 January ±49 days.

*Secondaries.*—There were three consistent foci for initiating molt of secondaries based on data from the SDNHM captive birds, specimens, and field observations: the tertials and secondaries 1 and 5 (S1 and S5, numbered proximally from outermost). Molt proceeded proximally from S1 and S5 and distally from the tertials, and it may become irregular in the area from S8 to S11. Six secondaries were retained from 1973 to 1978 on captive ASYs (SDNHM), two for one bird and four for the other individual. Combined locations of retained secondaries for the two birds were: S4, S7 (twice), S8 (twice), and S10. S1 dropped regularly in April followed by S2 and S5 in May and June, respectively. S3 and S6 usually dropped in June, S4 and S7 in July, S8 in August or September (but at times as early as mid-July), and S9 and S10 dropped between June and late September; S9 always dropped before S10. There was a tendency for molt to terminate at S11 and S12 with drop dates between May and June, and S12 following S11. Smaller secondaries (S1–S4) dropped together in April and May and as late as August. The tertiary feathers, as with the smaller secondaries, had a tendency to drop together between May and August with no discernable sequence.

There appeared to be some interannual variation in the number of secondaries retained. For example, 1979 was an atypical year of extraordinarily high numbers of retained feathers. One vulture retained five secondaries and two rectrices, another had nine secondaries and one rectrix retained that year. A possible reason is that the birds suffered from lead poisoning. The following year, after the birds had recovered from the apparent lead poisoning, no feathers were retained. Retained feathers dropped in May or June of the next year.

*Rectrices.*—Tail feathers generally had a consistent pattern for the six feather pairs (SDNHM). On one side, numbering rectrices from the central feather R1 to the outermost feather R6, the sequence was R1-R6-R2-R4-R3-R5. R1dropped between late April and May, R6 dropped regularly in May. The largest rectrix, R2, dropped in late May or June, followed by R4 in late June or July, R3 in July or August, and R5 in mid-August to early September. Tail feathers retained from the previous year dropped in May or early June of the next year. Three rectrices were retained during the first 6 years (1973–1978), a pair of R4s for one vulture and a single R5 for another.

*Feather Synchrony and Growth.*—Time elapsed between dropping of paired (right and left) feathers was calculated for P5 in captive birds at SDNHM. The average elapsed time was 7 1/2 days after the first of the pair had dropped (range 1–41 days). P1 and P6 through P10 held to this average or had an even shorter elapsed time, at times less than 24 hrs. P2 through P4 had the greatest range with an average of less than 10 days for P2 to an average of 1 month for P3 and P4. The maximum time for an individual feather was 41 days between drop dates for P3.

## DISCUSSION

Basic concepts of flight feather molt in diurnal soaring hawks, eagles, and Old World vultures have been presented by Miller (1941), Stresemann (1963, 1966), and Stresemann and Stresemann (1966). Later studies on wing molt by Brown and Amadon (1968), Houston (1975), Brown (1976), Edelstam (1984), Clark (2004), and Pyle (2005) have led to hypotheses about the role of flight feather replacement schemes that may be used to infer possible differences in flight strategies and aerial performance. Birds molt for specific reasons during certain times of the year and this molt is not random feather loss, but has a definite sequence that has an adaptive advantage in optimizing aerodynamics with respect to feather maintenance (Hedenstrom and Sunada 1999, Rohwer 1999, Pyle 2006).

Large birds exhibit several remigial replacement strategies detectable within a year and between years by wear patterns, contrasting feather appearance, and retained feathers (Pyle 2005, 2006, 2008). The most common strategy of molt among large birds that need to maintain flight, involves a *Staffelmauser* pattern meaning ''staggered molt'' (Stresemann and Stresemann 1966) and also known as ''stepwise molt''. Falconids typically replace all primaries and secondaries during each prebasic molt using multiple waves originating at P4 and S4, whereas larger accipitrids can retain primaries and secondaries from a previous season as part of a *Staffelmauser* sequence (Pyle 2005). The physiological demands of producing new feathers and the time required to complete a full molt are correlated to body mass and efficiency for flight requirements of larger birds (Shugart and Rohwer 1996, Pyle 2005). Sequential replacement of feathers in waves without having large gaps, increases the efficiency of wings and still allows larger birds to fly. A *Staffelmauser* pattern occurs in a wide range of larger birds, e.g., pelicans, herons, and condors (Pyle 2006, 2008).

As widespread and common as Turkey Vultures are throughout the Western Hemisphere, it is surprising that no comprehensive review has been published about their molt (but note comments and references by Kirk and Mossman 1998). For example, Stresemann and Stresemann (1966) mentioned that primaries are replaced irregularly, but Jackson (1988) correctly reported that, barring some aberrant irregular patterns, the molt takes place annually and within a single year, being replaced in a serial inner-to-outer sequence. Rea (1983) included findings by Chandler on secondaries and rectrices.

Our data produce a clearer picture of the flight feather molt of Turkey Vultures, which show similarities to other New World vultures, and the California Condor (Snyder et al. 1987). However, the molt of Turkey Vultures is more regular, more symmetrical between wings, and in a 1-year rather than the condor's 2-year cycle. There have been no comprehensive studies published on other cathartid vultures for additional comparisons or differences in molt in the Cathartidae.

Further comparisons of flight feather molt with other species of birds can be made in two ways, either by comparing molt in avian families related to the Cathartidae, or by comparing molt adaptations in other avian families that show morphological convergence with soaring flight. Unfortunately, the proximate affinity of cathartid vultures to other avian groups (e.g., Falconiformes or Ciconiiformes) remains unresolved (Ligon 1967, Rea 1983, Emslie 1988, Sibley and Ahlquist 1990, Avise et al. 1994, Helbig and Seibold 1995, Wink 1995, Livezey and Zusi 2007). The wing molt of Turkey Vultures, depending on phylogenetic relationships, may reflect an ancestral pattern. Molt patterns similar to those in Turkey Vultures are shared by some species of Ciconiiformes (Bloesch et al. 1977, Shugart and Rohwer 1996), a proposed ancestral group to Cathartidae. However, similarities in molt patterns are also seen in several other taxonomic groups, and are considered to be a widespread convergent molt adaptation in many taxa of larger soaring birds (Pyle 2006). Further data are needed to address this nature versus nurture issue.

*Molt Terminology*.—Turkey Vultures have an unusual pattern of primary replacement (Figs. 1, 2) that could be interpreted in several ways. One interpretation would be that the second molt cycle of SY birds involves replacement of P1–P3 (occasionally P1–P4) twice. This would necessitate labeling one of the replacements, either that of January–March or that of August–November, as a prealternate molt. Each successive prebasic molt typically would then begin at P4 (or P5) in the spring and finish with P1–P3 (or P1–P4) in the fall. However, prealternate molts are not known to occur among families thought to be close relatives of New World vultures.

A second interpretation would be that replacement of P1–P3 in SYs in the fall represents an advanced start to the third prebasic molt, concurrent with completion of the second prebasic molt. Each subsequent prebasic molt would then begin with P1 in the fall, usually (but not always) suspend for the winter, and resume with P4 in the spring (Pyle 2008). This is essentially a modification of *Staffelmauser*, in that all primaries are replaced in 1 year via two waves. Incomplete-to-complete replacement of the secondaries also appears to follow a *Staffelmauser*-like strategy found in other large birds (Pyle 2006). However, molt of primaries differs from text-book *Staffelmauser* in that replacement of P1 in the second wave is delayed until after the preceding wave has replaced the middle primaries; the molt assumes an annual regularity not found in other species exhibiting *Staffelmauser*. The advancement of some or all primary molt in selected species of a family, to occur before another life-history event (migration, breeding, chick-feeding), has been documented among loons, puffins, gulls, and diurnal raptors (Howell 2001, Howell and Pyle 2005, Pyle 2005). However, in these groups the second prebasic wing molt typically occurs or starts *later* in SYs than in subsequent ages, which is not the case in Turkey Vultures.

A third interpretation would be to treat the first wing molt of Turkey Vultures as a preformative molt and the molt of P1–P3 of SYs in the fall as the start of the second prebasic molt. The idea of a preformative molt being limited to flight feathers has not previously been recognized, but Howell (in press) has argued that *Staffelmauser* can develop in two ways. One is the conventional view that the first wing molt pertains to the second prebasic molt (a normal schedule), the other is that the process of *Staffelmauser* is kick-started by insertion of a preformative wing molt (an accelerated schedule). Species exhibiting accelerated schedules include Osprey (*Pandion haliaetus*), and most if not all Pelecaniformes (Howell, in press). The first wing molt in these species starts earlier than subsequent wing molts, which is also true of Turkey Vultures. To what extent normal and accelerated schedules reflect ancestral traits or environmental responses remains unknown.

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