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Abstract: Molt patterns of wild whooping cranes (*Grus americana*) are largely unknown, and what knowledge we have has been based on scant data. We documented patterns of feather molt in nonmigratory whooping cranes in Florida during 1993-2005. All birds replaced flight feathers (remiges) in a synchronous (simultaneous) manner and spent time flightless. It took 38-46 days (mean = 44 days, $n = 8$) for feathers to regrow and birds to regain flight ability. When flightless due to remigial molt, cranes became more secretive and spent more time in wetlands during feather regrowth. Most (70%) whooping cranes first molted their remiges at 3 years of age, 20% at 2 years of age, and 10% at 4 years of age. Birds never molted their flight feathers in consecutive years; instead they usually skipped 1 or 2 years between molts. Sets of flight feathers lasted 2-4 years (mean 2.5 years, $n = 41$). The remigial molt was seasonal; flight feathers were shed during 10 April-23 June, and contour plumage was molted later in the year (24 June-23 October). For 1-2 months in the summer prior to contour-plumage molt, whooping cranes took on a dingy gray appearance, but they appeared snowy white in autumn after the contour-feather molt.

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Little is known about the molt of whooping cranes (*Grus americana*). Most data available are for young (<450 days) captive birds (Stephenson 1971), which demonstrated that juvenile flight feathers are retained throughout this age. Older captive whooping cranes undergo a synchronous (simultaneous) molt of primary and secondary flight feathers (remiges) (Gee and Russman 1996). Whooping cranes of the Grays Lake experimental flock apparently underwent a simultaneous molt of flight feathers that rendered them flightless (R. Drewien personal communication). Data regarding remigial molt in the only self-sustaining flock (which breeds in and near Wood Buffalo National Park in Canada and winters in and near Aransas National Wildlife Refuge in Texas) are limited to a few opportunistic observations of shed primaries and secondaries (<12 per nest site) at nests late in the breeding season (B. Johns, personal communication).

The reintroduction of a nonmigratory flock of whooping cranes into Central Florida (Folk et al. 2008) presented an opportunity to collect information on molting in birds that were intensively monitored (>2-3 times/week for the life of the bird) and captured on a regular basis. Unlike at Wood Buffalo National Park, where whooping cranes are typically monitored only from the air, Florida's habitats allowed easier access for observations of the birds from the ground.

METHODS

We documented remigial molt of 71 whooping cranes by observing flight-feather length during routine monitoring of the flock from 1993 to 2005. We were unable to see some birds' flight feathers (flight feathers are hidden from view when the birds are not flapping or stretching their wings), but based on the birds' behavior, we determined they were molting. At the onset of remigial molt, the bird would typically undergo a rapid behavioral change. Birds normally were accustomed to project biologists and did not respond to their presence unless very closely approached. While molting, birds would react to biologists' approach at much longer "flushing" distances, typically walking or running away from the observer. We observed a subset ($n = 8$) of birds, for which we had complete data representing the time from ecdysis to complete regrowth, in order to describe the time necessary to regrow flight feathers. We observed another subset ($n = 30$) of birds immediately after their loss of remiges (prior to visible regrowth) in order to describe the seasonality of remigial molt.

Along with replacement of remiges, we also documented molt of body contour feathers. Birds ($n = 53$) handled for radio replacement and health-checks were examined for actively growing feathers.

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Figure 1. Secondary feathers on the right wing of a whooping crane show the contrast between the older frayed and yellowed feathers and a younger secondary feather (arrow).

RESULTS

Remiges

Each of the whooping cranes we observed underwent a synchronous (simultaneous) loss of flight feathers just as the new ones were growing in. Birds were observed to have either all or none of their flight feathers, and the feathers showed uniform wear. On several occasions we noted a single secondary feather--a "fresh" feather showing much less yellowing and wear than is typical of an older secondary feather--that apparently was younger than the other feathers (Fig. 1). Some individuals that initially appeared to be undergoing partial (incomplete or asynchronous) molts when captured were found to have feathers broken off rather than partially grown.

Whooping cranes in remigial molt underwent a flightless period during the time their flight feathers were regrowing. For the 8 birds for which we had well-defined dates of ecdysis (feather drop) and regrowth to full-length feathers, this time averaged 44 days (SD = 3.57, range 38-46). Cranes were reluctant to attempt to fly or even to spread their wings until flight feathers were at, or close to, their full length. Habitat use changed during remigial molt to include more time in marshes and lake edges, especially large marshes with dense emergent vegetation.

This behavior was "contagious" in that other members of the flock (or pair) that were not molting would take on the secretive and more aquatic nature of the molting bird(s), thus helping preserve the flock or pair bond. Some pairs separated during the molt season but usually reunited after the molt was complete.

Most (70%) whooping cranes first replaced their flight feathers at 3 years of age (Table 1), whereas a smaller group (30%) did so at 2 or 4 years of age. Remigial molt was seasonal and coincided with the anniversary of hatch dates for the birds; therefore, ages of the birds and their feathers were rounded to the nearest year. The second replacement of flight feathers most commonly took place at age 5, third replacement at age 8, and fourth replacement at age 10.

Table 1. Frequency, by age (in years), of nonmigratory whooping cranes undergoing simultaneous molt of flight feathers. The modal frequency for each successive molt is shaded.

	Age								
Molt	2	3	4	5	6	7	8	9	10
First	14 (20%)	50 (70%)	7 (10%)						
Second			2 (9%)	11 (48%)	9 (39%)	1 (1%)			
Third							4 (67%)	1 (17%)	1 (17%)
Fourth									2 (100%)

We never observed a bird replacing its flight feathers in consecutive years; instead they usually skipped 1 or 2 years between molts. Length of time between molts varied among birds and also varied for the same bird over time. For 71 whooping cranes we documented 14 different "patterns" of time between molts (Table 2). The mean time that a flight feather was retained was 2.5 years (n = 41 sets of feathers). Twenty-three sets of feathers were retained on the bird for 2 years, 16 sets for 3 years, and 2 sets for 4 years.

We saw no evidence that nonmigratory whooping cranes had any physical problems during feather regrowth. The condition and growth of feathers of birds captured after their molts were normal, and we saw no evidence of stunting or stress-bars that might indicate a nutritional problem. Broken

Figure 2. Left wing of a whooping crane with portions of secondary feathers missing (white area). These feathers were broken off under the wing coverts, but the bird could still fly.

Table 2. Age (in years) of 71 whooping cranes undergoing flight feather molts. Example: 5 birds molted at 3 and 6 years of age in line 8.

Molt				
First	Second	Third	Fourth	*n*
2				10
2	4			2
2	5			2
3				33
3	5			6
3	5	8		2
3	5	8	10	1
3	6			5
3	6	8	10	1
3	6	9		1
3	6	10		1
4				5
4	6			1
4	7			1
			Total	71

flight feathers were rarely seen. However, one unusual case involved a bird, captured 4 May 2000, whose secondary feathers were broken off under the wing coverts of both wings, effectively leaving the bird without any secondary feathers (Fig. 2). The bird was still capable of flight and was one of 2 birds carrying the same flight feathers for 4 years.

Ecdysis occurred during late spring to early summer (Fig. 3). The timing of the molt in relation to breeding is of interest. Our sample size was small, but of 4 pairs of whooping cranes that raised chicks to fledging, only 1 bird underwent remigial molt that year. This female went flightless in late May when the chick was 64 days of age. The female regained flight in mid-July after the chick had fledged (106 days of age). Apparently the periods of flightlessness of the adult and chick were overlapping.

Contour Plumage

Molt of contour plumage was also seasonal. Whooping cranes replaced the contour feathers every year between 24 June and 23 October (Fig. 4). In the early summer, birds began appearing more dingy and "gray" as their plumage aged (Fig. 5). By late fall, all whooping cranes were in their whitest plumage.

Rectrices

Our sample size for data regarding molt of rectrices is limited to 3 observations. Those 3 birds were replacing

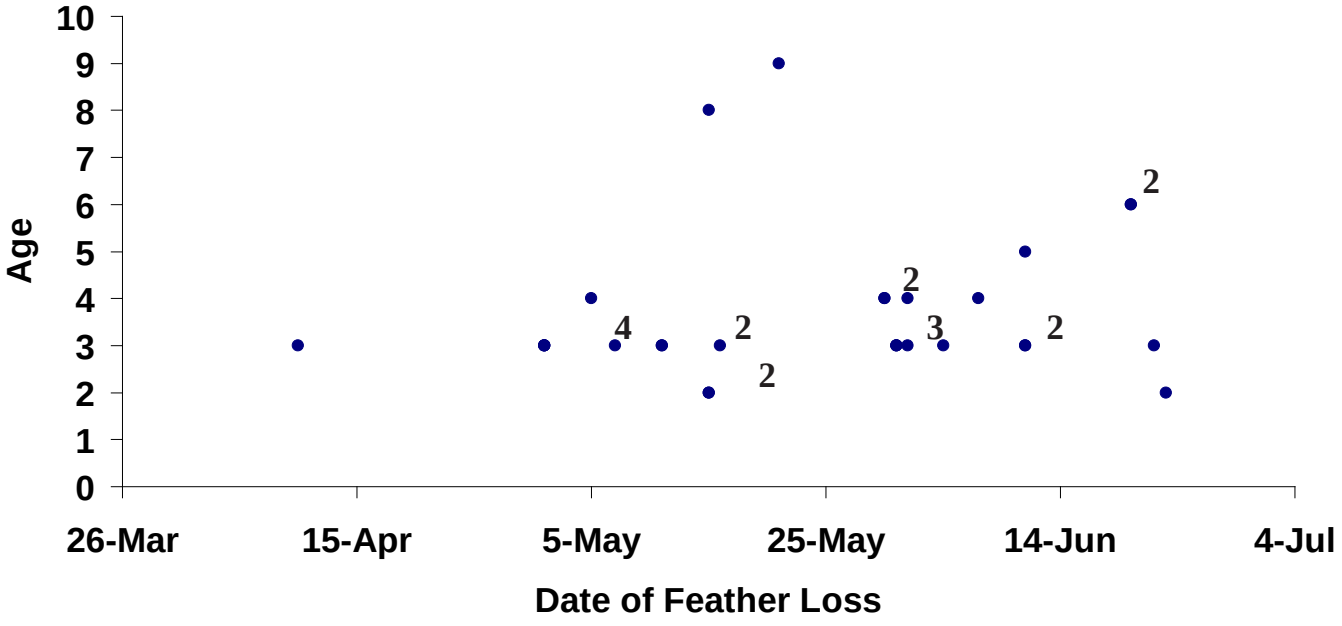

Figure 3. Dates that 30 nonmigratory whooping cranes in central Florida experienced remigial ecdysis.

some rectrices concurrent with replacement of body contour feathers. We do not know if they replace some rectrices every year.

DISCUSSION

Our findings confirm the somewhat speculative information reported by Allen (1952), that whooping cranes molt their flight feathers and body feathers at 2 different times, and that the birds undergo a flightless period. Erickson and Derrickson (1981) reported that whooping cranes first molt their primary feathers at 2 years of age and annually thereafter. In contrast, our results show that in Florida, only a small proportion (20%) of birds undergo their first remigial molt at 2 years of age, with most (80%) waiting until 3 or 4 years of age. Also in contrast, we determined that subsequent remigial molts were never annual, but usually ocurred every 2-3 years. Erickson and Derrickson (1981) said that it was uncertain whether all individuals become flightless during molt of the wing feathers. We found, without exception, that all whooping cranes underwent a flightless period during remigial molt.

Molt represents a physiologically demanding time in the life of birds (Welty 1982). Whooping cranes showed seasonality in both remigial and body contour-feather molts. Our data show that the latest day of the year when a whooping crane had shed its flight feathers (23 June) nearly coincides with the earliest day of the year when we have documented that a bird was replacing body-contour feathers (24 June). The time between these 2 demanding events probably serves to reduce the degree of stress to the body at a given time. Both molts took place during the time of year (late spring to early fall) when food resources should be most abundant.

In contrast to whooping cranes, Florida sandhill cranes (*Grus canadensis pratensis*) undergo an annual partial molt of flight feathers and do not become flightless. The median date for remigial ecdysis in Florida sandhill cranes was 2 June (Nesbitt and Schwikert 2008) and the median date for whooping cranes was 30 May. The median date for contour feather endysis was 24 August for Florida sandhill cranes and 20 August for whooping cranes. Florida sandhill cranes and whooping cranes undergo molts at similar times of year, but the sandhill cranes molt over a wider range of dates than the whooping cranes.

Whooping cranes have been described as "snowy white" (Lewis 1995). However, for 1-2 months in the summer just prior to molting, many individuals turn a light shade of gray (Fig. 5). During that time, the birds lose some consistency in the appearance of their plumage and appear rough or dingy, perhaps because of the contrast between the outermost heavily worn feathers and the fresher interior feathers beginning to show through. After molt the birds are back to

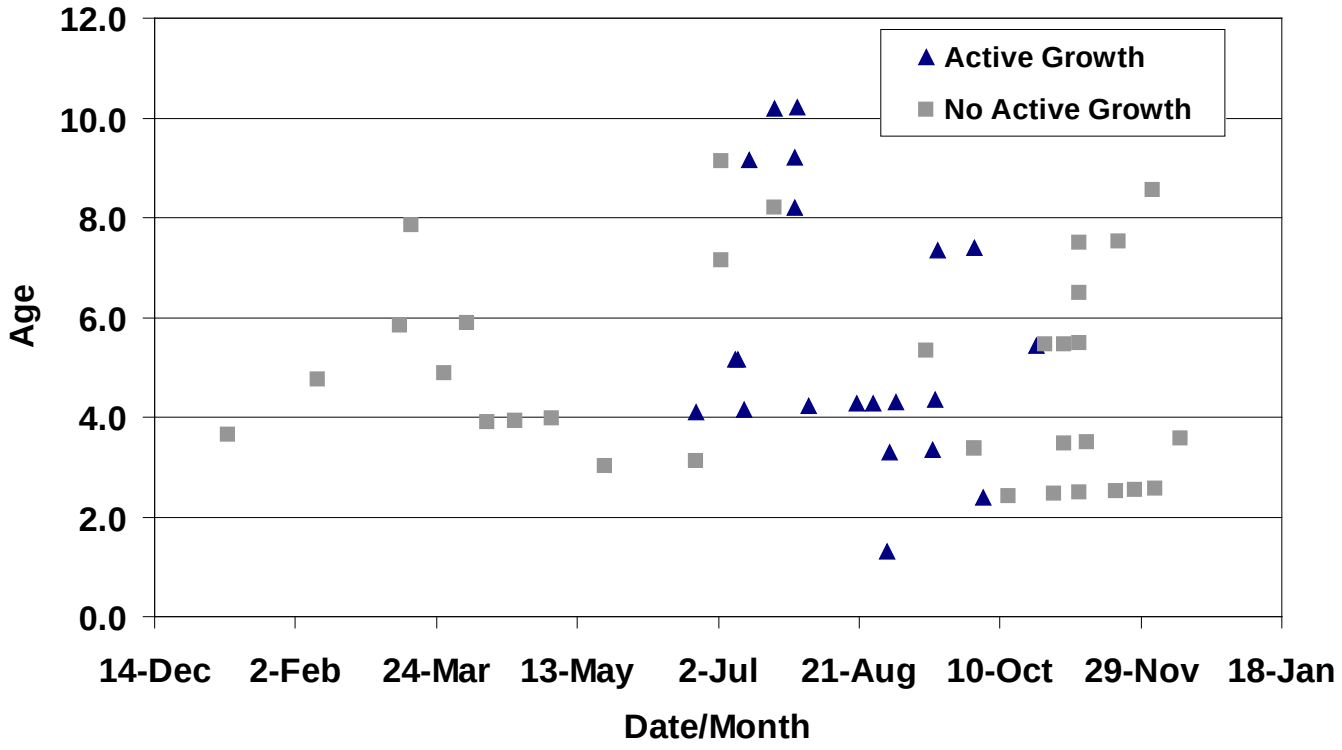

Figure 4. Dates at which 53 whooping cranes were either actively growing or not actively growing body contour feathers.

Figure 5. Contrasting appearances of whooping cranes, based on age and wear of contour plumage, just prior to contour-feather molt (bottom photo, adult bird on right) and during the rest of the year (top photo adult bird on left).

a very uniform white color.

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