

SERIAL DESCENDANT PRIMARY MOLT OR *STAFFELMAUSER* IN BLACK-CROWNED NIGHT-HERONS¹

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Abstract. Primary molt in Black-crowned Night-Herons (*Nycticorax nycticorax*) has been described as irregular. However, through an examination of museum specimens we determined that the molt of juvenal primaries progresses as a single descendant wave as primaries molt in sequence from primary 1 to primary 7 or 8. Molt then skipped to primary 10, the terminal primary, in most birds before the skipped primary or primaries were molted. The molt of juvenal primaries was arrested in 56% of specimens and a median of eight primaries was replaced (range 2–10). In contrast to the molt of juvenal primaries, 88% of adults had at least two descendant waves (range 1–4) of molt simultaneously active in primaries. Adults replaced from 2–10 primaries during a period of molt. The number of primaries replaced was bimodal with modes at 3.5 and nine. We were unable to track the transition from the single wave of molt evident in juvenal primary molt to the serial descendant waves in the adult primary molts. However, our findings for the juvenal and adult molts indicate that primary molt of Black-crowned Night-Herons is similar to serial descendant molt (*Staffelmauser*) in other species. Typically, serial waves in the adults arise through the arrest and continuation of descendant waves generated from a proximally located molt center. The variation in the number of primaries replaced by night-herons is evidence that the waves that typify serial descendant molt are simply a consequence of molt arresting due to time constraints on the length of the molt period. On the basis of available data for night-herons, serial descendant molt does not minimize the aerodynamic impact of primary molt or equalize the frequency of primary replacement.

Key words: *serial descendant molt; nycticorax; Staffelmauser; stepwise molt.*

INTRODUCTION

Sequential replacement of primaries allows birds to retain the ability to fly while molting. Sequential molt patterns are characterized by the point of origin for the molt sequence, or molt center, and by the sequence in which feathers are replaced. In the primaries, the most common pattern is descendant molt that starts at primary 1 (P1) and moves distally to the outermost primary (Ginn and Melville 1983). Many birds grow several primaries simultaneously which gives the appearance of a wave of molt.

Smaller-bodied non-passerine birds and most passerines replace all primaries in a single wave of descendant sequential molt. Typically, molt takes place on a yearly schedule starting from a single molt center at P1. Larger-bodied birds that retain the ability to fly while molting rarely renew all primaries during one year or molting season.

In larger-bodied birds the number of primaries molted has been correlated with the timing and length of the molting season. The length of the molting season is influenced by the timing of migration or breeding, breeding success, and sex of the individual (Ashmole 1968, Potts 1971, Houston 1975, Prevost 1983, Ginn and Melville 1983). In addition, there may be physiological constraints that limit the rate of feather growth and thus the rate of primary replacement (Prevost 1983).

When all primaries are not replaced, a new wave of molt may be generated from the molt center before the previous wave has reached the terminal primary. The result is a series of waves moving away from the molt center. In birds with descendant molt, this pattern has been termed serially descendant molt or *Staffelmauser*, and also stepwise molt (see Stresemann and Stresemann 1966, Ashmole 1968, Potts 1971, Prevost 1983, Ginn and Melville 1983, Rasmussen 1988).

A characteristic of serial descendant molt is the occurrence of newer primaries distal to older

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TABLE 1. Criteria used to age Black-crowned Night-Heron specimens and their primaries, and sample sizes used in this study.

Episode of primary molt (Humphrey-Parkes molt)	Age in months	Aging criteria	Sample size
First episode of primary molt (second prebasic molt)	12–15	Worn brown juvenal primaries, growing gray primaries, brown back	12
After first, before second episode of primary molt	15–24	Brown to gray back, mix of brown juvenal and gray primaries to all gray primaries	16
Second episode of primary molt (third prebasic molt)	24–27	Gray to black back, mix of brown juvenal and gray primaries to all gray primaries, primaries growing	3
Adults with primary molt (fourth and subsequent prebasic molt)	27+	Gray primaries, glossy black back	19
Adults without primary molt	36+	Gray primaries, glossy black back, primaries growing	19

primaries. Such a sequence arises when an arrested wave restarts in the medial or distal primaries. In a cursory examination of non-molting specimens of Black-crowned Night-Herons (*Nycticorax nycticorax*) we noted that many specimens had not replaced all primaries in the previous molt. Furthermore, many wings had series of new primaries located distally to older worn primaries. These observations were consistent with published accounts of primary molts in the Black-crowned Night-Heron and other Ardeidae that described molt as chaotic or irregular (Gross 1923; Palmer 1962; Stresemann and Stresemann 1966; Siegfried 1971; Kokshaiski, cited in Milstein et al. 1970; Cramp and Simmons 1983). But, our observations were also consistent with serial descendant molt (see Ashmole 1968, Potts 1971, Prevost 1983, Ginn and Melville 1983). In this paper we examine Black-crowned Night-Herons to determine if they replace primaries in a serial descendent pattern.

METHODS

Most of the specimens used for this study were collected from the Potholes Region, Grant County, Washington and are preserved at the University of Washington Burke Museum. Additional specimens were borrowed to supplement the Burke specimens (see Acknowledgments).

This manuscript deals with the origin, direction, and number of primaries molted during episodes of primary molt. In Table 1 we provide the formal names for the molts (Humphrey and Parkes 1959) associated with episodes of primary molt. We used the informal "episode of primary molt" rather than standard terminology to min-

imize confusion surrounding the first episode of primary molt. During this molt, which occurs when night-herons are 12–15 months of age, juvenal primaries are lost and replaced for the first time. However, referring to the first molt of primaries as the "first prebasic primary molt," which occurs during the second prebasic molt, or the "postjuvenal primary molt," which occurs during the first postnuptial molt, is confusing and incorrect (Rohwer et al. 1991). We refer to the episodes of primary molt as first, second and adult (third and subsequent) (Table 1).

To quantify the origin, direction, and number of primaries molted during episodes of primary molt, we first needed to establish the age of primaries. In the first episode of primary molt, new gray primaries replace old brown juvenal primaries. This color difference, in combination with body plumage (Table 1), allowed us to accurately age primaries. For other primary molts, we aged primaries by scoring feathers for wear and fading. For specimens in active molt, the length of each growing primary was estimated to the nearest tenth of its estimated total length. The growing primaries provided a benchmark from which to judge wear and fading. Primaries that were similar to growing feathers were judged newly replaced and were assigned a score of 0. By comparison to growing and new (category 0) primaries, the remaining primaries were scored 1, 2, or 3, depending on the amount of wear and fading. For specimens that were not in active molt there was no benchmark. Scores for least wear/fading, medium wear/fading, extreme wear/fading were 1, 2, and 3, respectively. Data are provided in the Appendix 1.

We determined the direction of molt in adults by comparing the length of each growing primary to its neighbors (Houston 1975, Langston and Rohwer 1995). For a growing primary the direction of molt can be inferred in three different situations. 1) If two adjacent primaries are growing, the direction is from the longest to shortest. In this circumstance, we arbitrarily used the proximal growing primary as the focal feather. 2) If a growing primary's distal neighbor is old (class 1, 2, or 3), direction is from the growing to the distal primary if the growing primary's proximal neighbor is also growing or new. If the proximal primary is old, the growing feather is isolated among old feathers and no direction can be inferred. 3) If a growing primary's distal neighbor is new (class 0), the direction is from the distal primary to the growing primary. In these comparisons we assume similar growth rates of adjacent feathers. If both wings were preserved, we used the wing with more growing primaries, or the left, if both wings had the same number of growing primaries. Additional summaries using age differences in primaries were done to test specific assumptions regarding the restarting of arrested waves, the original initiation point of waves, and the synchrony in the start of waves.

An analysis of the number of primaries replaced in adult molts required estimating the length of the molting season and the growth rate of primaries. The length of the molting season was estimated from the state of molt in museum specimens and from observations of wild birds. We also computed molt scores to document the progress of molt by date. Scores were computed as a count of the number of new and growing primaries per wing and as the mm of growth per wing. The mm score is the sum of the length in mm of new and growing primaries. Mean lengths, which were obtained by measuring the length of primaries in five birds of each sex, were used to estimate the length in mm of each primary. The mm score takes into account differences in length of primaries.

We estimated primary growth rates using growth bands. Growth bands are alternating light and dark bands. Each pair of bands is thought to reflect a day's growth of feathers (Michner and Michner 1938, Grubb et al. 1991). In Black-crowned Night-Herons, growth bands were visible in only one or two primaries per individual. For these primaries, we divided the longitudinal length of a series of a minimum of four pairs of

bands by the number of pairs to estimate the mm of primary produced per day. If bars were obvious on two primaries in one wing, we used an average of the two rates.

RESULTS

FIRST EPISODE OF PRIMARY MOLT

Of 12 specimens that were molting juvenal primaries, nine had series of new gray primaries in the proximal and medial wing and worn brown primaries in the distal wing. Five of the nine were symmetrical in having replaced primaries proximal to a single growing feather at P2 (UWBM 30,990), P3 (UMMZ 74,228, FMNH 324,608) and P7 (PSM 20,779, UMMZ 120,609). The distal location of the growing feather in a series of new primaries indicate a proximal to distal, or descendant, direction to the molt. Two of the nine specimens (FMNH 156,309, FMNH 156,311), which were collected on the same day, had replaced P1-P3 in both wings. There were no primaries growing in either wings of FMNH 156,309 and in the left wing of FMNH 156,311. However FMNH 156,311 was growing P4 on the right suggesting that its left wing and both wings of FMNH 156,309 were still molting rather than having arrested. The remaining two of the nine specimens had multiple primaries growing within a wing. In FMNH 52,424's left wing, P1-P4 were new and P5, which was growing, was more advanced than P6, which had not emerged from the skin. Only P6 was growing in the right. UWBM 47,800 had replaced P1-P3 and P4, P5, and P6 were 0.9, 0.4 and 0.1 of their relative lengths, respectively, indicating a descendant sequence of molt in each wing.

Once P1-P6 were replaced and as P7 was almost fully grown, the remaining primaries were replaced out of sequence in some specimens. The three molting specimens, in which molt had progress beyond P7, illustrate this out-of-sequence molt. In one of the three (UWBM 50,435), P7 in both wings was 0.9 of its total length. In the right wing, P10 was growing and had reached half its total length. Thus, in this wing, molt must have skipped from P7 to P10 when P7 was about half grown. In the second specimen (UWBM 46,737), P7, P8, and P10 were growing and P9 had been skipped in both wings. Relative lengths for P7, P10, and P8 were 0.8, 0.7, 0.5, respectively, indicating the sequence of replacement. The third bird (UWBM 32,676) was following a

similar pattern, but was more advanced; P7 and P10 were fully grown and P8 and P9 were growing. Relative lengths were 0.9 for P8 and 0.6 for P9 indicating a sequence of P7, P10, P8, then P9.

Two of 16 non-molting specimens that had arrested this primary molt provided additional evidence that the molt skips some distal primaries. Both specimens arrested molt after replacing all juvenal primaries but omitted P9 (UWBM 42,461) and P8–P9 (CMNH 120,628). However, one (UMMZ 93,999) of the 16 did not skip P8, but replaced P1–P8 in the right wing before arresting molt. The remaining non-molting specimens arrested molt at or before P7 (six specimens) or replaced all primaries (seven specimens) thus obscuring the sequence of replacement.

We infer that the first episode of primary molt starts at P1 because this molt of primaries included P1 in all 12 molting birds and 16 non-molting birds that were collected after the first but before the second episode of primary molt. However, only one specimen (UWBM 30,990), in which P1 was new and P2 was growing, excluded all other possible starting points. In two other molting specimens (UMMZ 74,228, FMNH 324,608), P1 and P2 were new and P3 was growing, which excluded all possibilities except P1 and P2. Thus, we conclude that the first episode of primary molt proceeds in sequence from P1 to P7 or P8. Molt then skips to P10, then P8 (if omitted), and lastly P9.

Our sample of birds that had completed the first episode of primary molt consisted of 16 specimens from widespread localities in North America. A median of eight primaries were replaced (range 2–10) and molt was arrested in 56% (9/16).

SECOND EPISODE OF PRIMARY MOLT

Specimens in this molt were rare in collections and we examined only three molting birds. These specimens are noteworthy, nonetheless, because they illustrate patterns of primary molt that could be induced by the variability in the first episode of primary molt. One specimen (UWBM 47,809) was starting this molt of primaries at P1. It had retained no juvenal primaries and all gray primaries were worn, so it must have replaced all primaries in the first episode of primary molt. In the second specimen (UMMZ 84,634), molt was starting at P1 and P8. P9 and P10 were old ju-

venal primaries meaning that the first episode of primary molt arrested after P1–P7 were replaced. The third bird (UWBM 47,807) was beginning molt at P1 and P9, however P10 was gray, but worn, indicating that it had been replaced in the first episode of primary molt. Thus, this specimen must have replaced P1–8 and P10 omitting P9 in the first episode of primary molt.

PRIMARY MOLT OF ADULTS

We examined 19 adult specimens that were growing primaries. Of these, 15 had series of new and growing feathers separated by older worn primaries that had not been replaced. Six specimens were growing primaries in three distinct series and nine had two distinct series. Of the four specimens with only one series, in two (UWBM 42,466, UWBM 47,810), all the primaries were old except for P1, which had just started growing. For these two specimens molt had just started and it may have been too early in molt for separate series to be evident. Thus, excluding the two specimens early in molt, 88% (15/17) of the Black-crowned Night-Heron adults were simultaneously molting primaries in distinct series.

In the series of new and growing primaries, there were 40 growing primaries that provided information that was useful in assessing the direction of molt. Eighty-eight percent (35/40) of the growing primaries had begun growing before the distal neighbor thus indicating that molt was progressing in a proximal to distal, or descendant, direction (Table 2). Because a descendant direction of molt was evident, we are justified in referring to these series as descendant molt waves.

We have shown that there can be several descendant waves of molt simultaneously active in Black-crowned Night-Heron primary molt. We assume that these waves that start distally to P1 were restarting after having arrested in a previous molt and that these waves originated from a molt center at P1 (Potts 1971, Prevost 1983). These assumption are difficult to verify with museum specimens, but the following evidence suggests they are valid for Black-crowned Night-Herons.

We first consider our assumption regarding the restart of arrested waves. If waves were restarting after having arrested, then the starting points for waves should be distributed across all primaries rather than concentrated at a few set initiation points or molt centers. To evaluate this assumption, we assumed that the initiation point for a

TABLE 2. Locations in the wings of 50 growing primaries used as the focal points to determine the direction of molt in 19 adult Black-crowned Night-Heron wings. Direction is relative to the growing primary.

	Primary number									Total	
	1	2	3	4	5	6	7	8	9		
Distal neighbor was growing, direction was:											
descendant (proximal to distal)		3	3	2	2	1		1	1	13	
ascendant (distal to proximal)				1						1	
undetermined (tied)	2								1	3	
Distal neighbor old, proximal neighbor new or growing, direction was:											
descendent	6*	3	2	2	4	1	2	1	1	22	
Distal neighbor new, direction was:											
ascendant	1*									1	
Distal and proximal neighbors old, direction was:											
undetermined			2		1	1	1	2	3	10	

* Growing primary 1's were compared only to the distal neighbor.

wave was the proximal primary for each series of new and growing feathers. A count of these initiation points indicates that molt can start at every primary (Fig. 1).

Our second assumption was that waves were generated originally from P1. If true then P1 should have been replaced in all wings. For adults that were not molting, P1 was the only primary that had been replaced in the previous molt by all specimens (Fig. 2). In molting specimens, 79% (15/19) were growing or had renewed P1s in the present molt. In the four specimens that had not renewed both P1s, two molted P1 in one wing (UWBM 47,804, UWBM 47,806). In the other two specimens a wave of molt appeared to have started at P2 (UWBM 47,803) and at P2 in the right and P3 in the left (UWBM 47,811). However, because P1 had been replaced in all birds that had finished molt, but not yet in all the birds that were molting, this means that molt at P1 began after the onset of molt in at least 21% (4/19) of night-herons.

To further quantify the timing of molt in the proximal primaries, we compared the relative lengths of P1 to P2 and to P3 in specimens that were growing these primaries. For the cases in which a determination could be made (see Table 3), P1 was shorter, and thus molted after P2 in 23% (3/13) and after P3 in 33% (5/15) of the specimens (Table 3). Earlier onset of molt distal to P1 likely indicates that an arrested wave in close proximity to the molt center has precedence. Alternatively, there may be a distal shift in the molt center in some birds (see Langston and Rohwer 1995). Unfortunately, data available do not allow to us to evaluate these possibilities.

The variability in the start and progression of molt at the various points in the wing is illustrated by the six specimens with three waves (Fig. 3). In UWBM 47,788 and UWBM 47,795, three waves appeared to have started synchronously. These two specimens differ in that UWBM 47,795 is growing only one primary per wave while

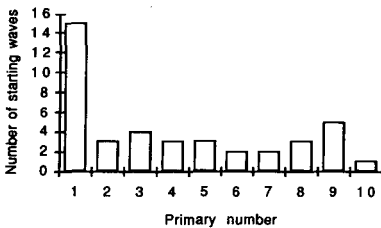


FIGURE 1. Initiation points for waves (n = 41) in the left wings of 19 Black-crowned Night-Herons that were molting primaries.

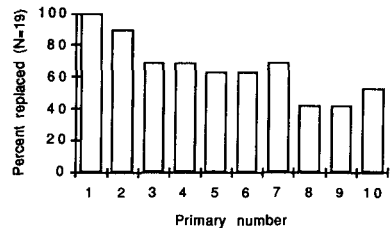


FIGURE 2. Frequency of replacement of individual primaries in 19 adult Black-crowned Night-Herons. The left wing was used unless only the right was preserved.

TABLE 3. Estimated start of molt in primary 1 in relation to primary 2 and primary 3. The category of "Undetermined" indicates that a determination could not be made because primaries under comparison were fully grown or had not been replaced.

	Primary 1			Undetermined
	Earlier	Tied	Later	
Primary 2	9	1	3	6
Primary 3	10	0	5	4

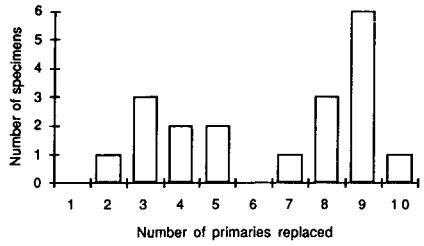


FIGURE 4. Bimodal distribution in the number of primaries replaced by 19 adult Black-crowned Night-Herons from eastern Washington. The left wing was used unless only the right was preserved.

UWBM 47,788 started molt of two primaries in the proximal and distal waves. In UWBM 50,435 and UWBM 47,802, one feather had been or was almost grown in each wave. A second primary was growing in each of three waves in UWBM 50,435 and in the distal and medial wave of UWBM 47,802. In contrast, in the medial wave of UWBM 47,794 and PSM 19,951, one primary

was fully grown and two were growing while in proximal and distal waves, at most, only one primary had grown. Of the six specimens, two each had two, three, and four waves in the wing not pictured in Figure 4.

We quantified the variability in the number of primaries replaced by adults using specimens

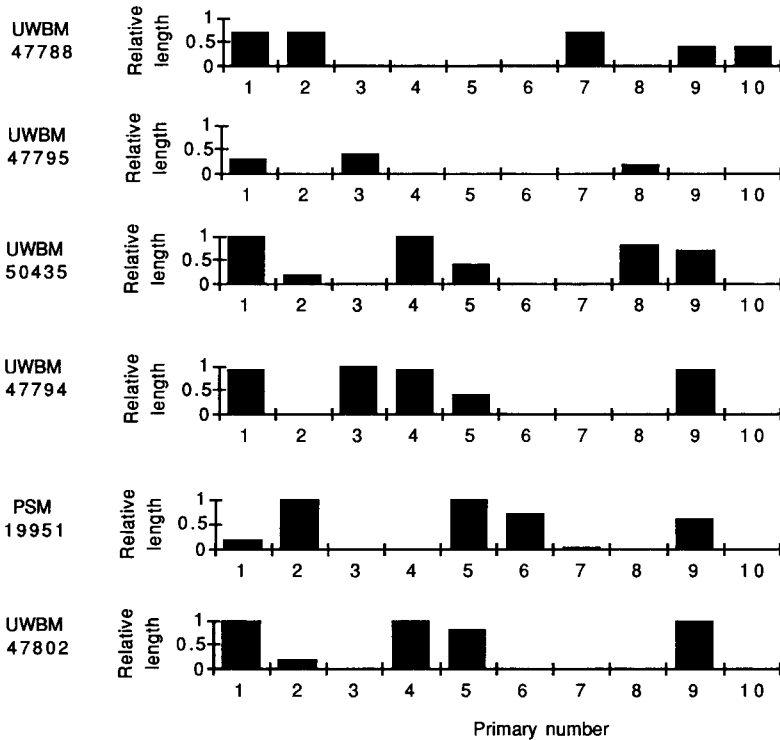


FIGURE 3. Initiation points and progress of molt waves in the six Black-crowned Night-Heron specimens with three waves of molt. Black bars represent the proportional length (y-axis) of new and growing primaries. Old primaries are indicated by no bar. The left wing was used unless there were more growing primaries in the right.

TABLE 4. Length of primaries in mm from the estimated point of attachment to bones of the hand to the primary tip. Five sets of primaries for each sex were measured.

Primary	Female	Male	Combined
1	187	190	188.5
2	199	199	199.0
3	205	208	206.5
4	211	217	214
5	221	229	225
6	228	238	233
7	237	243	240
8	235	240	237.5
9	231	236	233.5
10	226	226	226
Total length			2,203

from one locality in eastern Washington. This is the one site from which we have large samples of molting and non-molting specimens. Counts of the newest primaries in the non-molting specimens indicate that the number of primaries replaced per molt was bimodal with modes at 3.5 and nine (Fig. 4). The variation in the number of primaries replaced could reflect individual differences in the time available for molt or in rates of primary growth. We examined these factors below.

We estimated the time available for molt in eastern Washington using the occurrence of molt in museum specimens supplemented with observations of wild birds. Of the adults collected in May or June, only 15% (2/13) were molting. One (UWBM 42,466) had just begun growing P1

on 15 June while the second (UWBM 42,474) had renewed P1–P3, and was growing P4–P5 on the left and P4 on the right on 22 June. UWBM 42,474 probably began molting in May. By July, 50% (6/12) of specimens had initiated primary molt, and 100% (13/13) of those collected in August through the first week of September were molting or had completed or arrested molt. The earliest date for the completion of molt was 23 August (PSM 12,024). By 6–7 September 1991, most adults had left the area so we were unable to determine when the birds stopped molting. Assuming that molt continues until migration starts in September, the maximum time for primary molt would be about 20 weeks (May through September). However, our data indicate that many birds do not start molt until late July, which would leave only eight weeks if molt continued through September.

Although most birds were molting primaries by August, molt scores, which indicate what proportion of the primaries were replaced for individual birds, were not significantly correlated with date (Fig. 5). The lack of a correlation indicates that many birds are in an early stage of molt late in the season.

We estimated that the mean primary growth rate was 6.0 mm/day (SE = 1.8 mm, range = 2.7, 9.0 mm) for the 23 individuals in which growth bars could be seen. These measurement must be interpreted cautiously because they are from only one or two primaries per individual and bars were not visible in all specimens. Nonetheless, they do illustrate that some variation in growth rates can be expected. These values are within the known rates of primary growth (Prevost 1983) and provide estimates of a mean and range for calculating the time it would take to replace all primaries (Fig. 6).

By growing one primary per wing at a time, even at the maximum growth rate, a bird could not replace all primaries in the estimated 20 week maximum molt season (Fig. 6). However, in the 19 adults that were growing primaries, a median of three primaries were simultaneously growing per wing. Four specimens were growing only one primary, five each were growing two and three, three were growing four, and two were growing five. The wing with the greatest number of growing primaries was used. However, the median is probably conservative because some birds were just starting molt while others were finishing. For example, of the four bird growing only one pri-

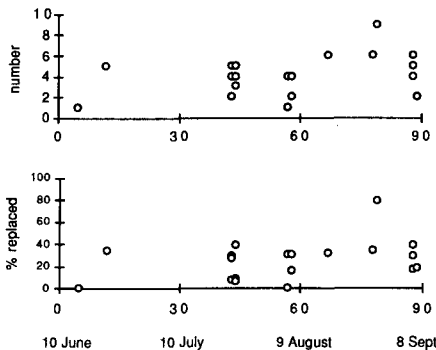


FIGURE 5. Molt scores for 19 Black-crowned Night-Herons that were molting primaries. The x-axis is the days from 10 June. Pearson r 's for A) .3, $P > 0.05$, $n = 19$ and B) .3, $P > 0.05$, $n = 19$.

mary, two were just starting molt and one was finishing. By growing primaries simultaneously at a median of three primaries per wing, a complete set could be grown in about 17.5 weeks (Fig. 6). By growing more primaries simultaneously, by increasing rate of growth, or both, birds could replace all primaries in less than 10 weeks.

DISCUSSION

Primary molt of Black-crowned Night-Herons is similar to serial descendant primary molt in other species. Typically, serial descendant molt starts with a first molt that is an ordinary sequential descendant molt consisting of a single wave moving in a proximal to distal direction through the primaries (Ashmole 1968, Potts 1971, Prevost 1983, Rasmussen 1988). We found that the first molt of Black-crowned Night-Herons was similar to this. The first molt progressed sequentially as a single wave from P1 through P7 or P8, then skipped to P10 in some birds, before the skipped primaries were molted. The significance of the out-of-sequence molt is unclear, but it also has been documented in the first molt of shags (*Phalacrocorax* sp.), which as adults, molt primaries in serial descendant waves (Rasmussen 1988).

In adults of species with serial descendant molt, a series of "roughly parallel waves" move in a descendant direction through the primaries (Stresemann and Stresemann 1966, Ashmole 1968, Snyder et al. 1987). The serial waves arise when a wave of molt arrests then continues during the next molt period as a new wave is generated from a molt center in the proximal primaries. By the second period of molt it is possible to have two waves and three waves by the third period of molt. However, the number of waves will depend on the number of primaries molted in each wave prior to an arrest (Potts 1971, Prevost 1983). In most of the adult night-herons in our study, there were series of two or more waves of descendant molt simultaneously active in primaries within individual wings. Although we were unable to document the transition from the first molt to adult molts, it is likely that the serial waves in night-herons arise in a manner similar to other species. This conclusion is reasonable given the evidence from other species (Potts 1971, Prevost 1983, Rasmussen 1988) and from our finding that the first molt proceeded as a single wave of descendant molt that can arrest.

The degree of asynchrony in the start or restart of molt within some of individual adult night-

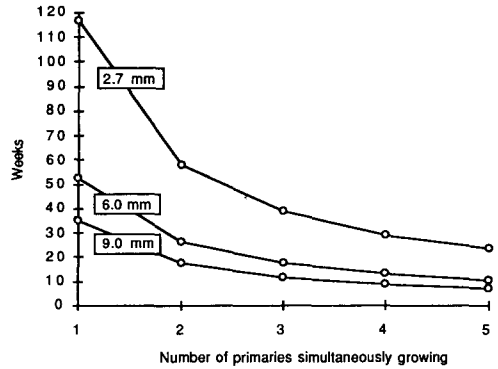


FIGURE 6. Differences in the estimated time in weeks to grow all 10 primaries per wing (2,203 mm in length) assuming constants for minimum (2.7 mm/day), mean (6.0 mm/day), and maximum (9.0 mm/day) growth rate per primary.

heron wings is typical of serial descendant molt. Similar asynchrony and distortion of the idealized pattern of "roughly parallel waves" was evident in Ashmole's (1968) model study with White Terns (*Gygis alba*), which first documented the continuation of serial waves after an arrest of molt. In adult White Terns, after an arrest of molt, waves started asynchronously in individual's wings. In the four individuals for which the start of molt was documented after an arrest, the onset of molt did not include P1, which was the presumed molt center (Ashmole 1968). Ashmole also suggested that the advance of waves slowed as they reach the longer distal primaries, which would allow a medial wave to catch up to a distal wave and combine. This occurred because the shorter proximal and medial primaries grow in less time than the longer distal primaries (Snyder et al. 1987). Waves also advanced a variable number of primaries per wave. Based on Ashmole's original study of the phenomenon, studies documenting the ontogeny of serial waves (Potts 1971, Prevost 1983, Snyder et al. 1987), and our study of night-herons, serial waves will not be evident until after an arrest of molt. After several arrests, the existence of serial waves will give the impression that waves are moving roughly in parallel through the primaries. But as the bird ages, the parallel structure may be distorted due to asynchrony in the arrest, restarting, and generation of waves. In addition, individual differences in the number of primaries replaced during a period of molt will result in variation in the number of primaries renewed in each wave

and how far each wave advances through the primaries. Thus, after the first few molts, although serial descendant waves will be evident, the pattern and progression will exhibit extreme variation.

The individual variation in the number of primaries molted and point of arrest that we documented in night-herons impinge on adaptive interpretations of the phenomenon. Generally, it is assumed that aerodynamical benefits are important in the evolution of serial descendant molt. Serial waves disperse growing feathers throughout the primaries, thereby creating several small gaps relative to a large gap that would be created by replacing a similar number of primaries in a single wave. Thus, serial waves allow a bird to simultaneously replace primaries with a minimal effect on the aerodynamics of flight (Ashmole 1968, Prevost 1983). This rationale provides the basis for what we refer as the aerodynamic hypothesis. An implicit assumption of the aerodynamic hypothesis is that the arrest of the first few molts serve as the mechanism to set up serial waves. The aerodynamic hypothesis can be rejected for Black-crowned Night-Herons because only 56% of the specimens arrested the first episode of molt. When molt did arrest, the point of arrest varied from P2 to P10. If aerodynamic benefits were significant, we would expect most birds to arrest the first episode of molt and that there would be more consistency in the point of arrest. Alternatively, the variability in the number of primaries replaced and in the point of arrest during the first episode of primary molt appears simply to be a function of the time available for molt.

Similarly, the wide range from 2–10 primaries replaced and the bimodal distribution of replacement by eastern Washington night-herons provides further evidence that the number of primaries molted is simply a function of the time available. Based on our estimates of the time it would take to molt, the higher mode of nine may represent birds that molt for 8–10 weeks after breeding and before migration. It may also include some non-breeders or failed breeders that molted for an extended period of time. The low mode of 3.5 primaries may be those birds that started late in the season. The modes could also be influenced by individual differences in primary growth rates.

As an alternative to the aerodynamic hypothesis, we suggest that the serial waves that typify

serial descendant molt simply are the consequence of insufficient time for molt. We refer to this alternative as the time constraints hypothesis. Evidence for this hypothesis is the individual variation in the number of primaries molted. The result is individual variation in the point or points of arrest, and ultimately, in the pattern of serial waves that typify serial descendant molt.

For individuals that are unable to replace all primaries in a molt season, the ability to arrest a wave and then continue during the next period of molt may be adaptive in ensuring that primaries that were not replaced during a molt will be the first in line for replacement in subsequent molts (Ashmole 1968, Prevost 1983, Snyder et al. 1987). The capability could equalize the frequency of primary replacement in birds that are unable to replace all primaries during a period of molt. However, an enigmatic feature of serial descendant molt is that proximal primaries are replaced more frequently than distal primaries, which seems counter to the assumed function of arrested molt. The disparity in the frequency of replacement occurs because a new wave of molt is generated during each period of molt before existing waves have coursed through the primaries. In the first few periods of molt, the proximal primaries can be replaced several times before the distal primaries are replaced once (Potts 1971, Prevost 1983). This tendency appears to persist in adult night-herons. For example, we found that 100% of the specimens had replaced P1 and 90% replaced P2 in the previous molt which means that these inner primaries were replaced almost every year. By contrast, P8–10 were replaced in about 50% of the specimens suggesting that these primaries are replaced every other year. The apparent inefficiency of replacing proximal primaries more frequently, or conversely, of replacing distal primaries less frequently, appears to be provide additional evidence that serial descendant waves are simply a consequence of arrested molts due to time constraints. Thus, in Black-crowned Night-Herons, serial descendant molt does not appear to be a molt strategy evolved to equalize the frequency of primary replacement.

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