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ORNAMENTAL PLUME DEVELOPMENT AND THE ''PREALTERNATE MOLTS'' OF HERONS AND EGRETS

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ABSTRACT.—To investigate molts and ornamental-plume development in herons and egrets, we examined 448 specimens of 10 North American species. We found no evidence for a prealternate molt, despite widespread opinion that such a molt occurs and includes the ornamental plumes. Our data indicate that these plumes emerge during the later stages of the definitive prebasic molt in August–November, grow slowly through January–February, and are retained until replacement during the following prebasic molt. The preformative (traditionally termed ''first-prebasic'') molt shows substantial variation in extent. In 91.9% of 86 first-year individuals collected between November and May, this molt included the development of ornamental plumes that were similar in form, but shorter in length, than those of adults. Male Great Blue (*Ardea herodias*) and Little Blue (*Egretta caerulea*) herons developed longer ornamental plumes than females, presumably a result of sexual-selection strategies. *Received 9 February 2004, accepted 28 September 2004.*

Herons and egrets (Tribe Ardeini) are widely regarded as having two plumages per year—a ''non-breeding'' or basic plumage in fall and winter, and a ''breeding'' or alternate plumage in spring and summer (Palmer 1962, Cramp 1977, Hancock and Kushlan 1984, Marchant and Higgins 1990, Voisin 1991). The extent of ''pre-breeding'' or prealternate body-feather molts reportedly varies from at least a few crown feathers in Great Blue Heron (Palmer 1962; see Table 1 for scientific names) to complete in Great Egret, Cattle Egret, and Black-crowned Night-Heron (Witherby et al. 1939). The ornamental plumes have been considered part of the alternate plumage, with shorter basic ornamental plumes reportedly being replaced by longer alternate plumes in spring (Palmer 1962, Telfair 1994).

By definition, the occurrence of a prealternate molt requires the activation of follicles more than once during the molt cycle (Humphrey and Parkes 1959). In north-temperate herons and egrets, therefore, an early spring molt (additional to the annual prebasic molt) has been presumed, involving the replacement of basic ornamental plumes along with varying proportions of basic contour feathers. In order to confirm the existence of prealternate molts and determine the occurrence and length of basic and alternate ornamental plumes in herons and egrets, we examined 448 specimens of the 10 species that breed in North America north of Mexico.

METHODS

Specimens of herons and egrets were examined at the California Academy of Sciences (CAS), San Francisco; the Museum of Vertebrate Zoology (MVZ), Berkeley; the British Museum of Natural History, Tring; the American Museum of Natural History, New York; and the B. P. Bishop Museum, Honolulu. All specimens were collected in Canada, the United States, and northern Mexico, presumably

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TABLE 1. Number of North American heron and egret specimens examined and proportion of each sample collected during active molt, by season and age.[a]

Species	Age[a]	Jul–Aug *n* (%)	Sep–Oct *n* (%)	Nov–Dec *n* (%)	Jan–Feb *n* (%)	Mar–Apr[b] *n* (%)	May–Jun[b] *n* (%)	Total[c] *n, n*
Great Blue Heron	AD	3 (0.3)	8 (0.9)	7 (0.1)	7 (0.0)	25 (0.0)	17 (0.1)	67, 13
(*Ardea herodias*)	1Y	3 (0.0)	5 (0.2)	5 (0.4)	13 (0.2)	7 (0.0)	2 (0.0)	35, 6
Great Egret	AD	5 (0.2)	5 (1.0)	5 (0.4)	3 (0.0)	8 (0.0)	1 (0.0)	27, 8
(*Ardea alba*)	1Y	3 (0.0)	7 (0.4)	3 (0.3)	3 (0.3)	1 (0.0)	4 (0.0)	21, 5
Snowy Egret	AD	2 (1.0)	0 (—)	4 (0.3)	1 (0.0)	4 (0.0)	3 (0.0)	14, 3
(*Egretta thula*)	1Y	6 (0.0)	5 (0.4)	0 (—)	0 (—)	3 (0.0)	2 (0.0)	16, 2
Little Blue Heron	AD	5 (0.6)	3 (1.0)	2 (0.0)	5 (0.0)	5 (0.0)	7 (0.3)	27, 8
(*Egretta caerulea*)	1Y	0 (—)	0 (—)	0 (—)	1 (0.0)	2 (0.0)	3 (0.0)	6, 0
Tricolored Heron	AD	2 (1.0)	1 (1.0)	2 (0.5)	3 (0.0)	1 (0.0)	2 (0.0)	11, 4
(*Egretta tricolor*)	1Y	2 (0.0)	4 (0.5)	2 (0.0)	2 (0.0)	1 (0.0)	1 (0.0)	12, 2
Reddish Egret	AD	2 (0.0)	1 (1.0)	4 (0.3)	1 (0.0)	6 (0.0)	2 (0.5)	16, 3
(*Egretta rufescens*)	1Y	1 (0.0)	4 (0.3)	2 (0.5)	1 (0.0)	0 (—)	2 (0.0)	10, 2
Cattle Egret	AD	3 (1.0)	0 (—)	3 (0.0)	2 (0.0)	2 (0.0)	4 (0.3)	14, 4
(*Bubulcus ibis*)	1Y	0 (—)	0 (—)	6 (0.3)	0 (—)	1 (0.0)	6 (0.0)	13, 2
Green Heron	AD	9 (0.8)	7 (0.9)	2 (0.0)	2 (0.0)	6 (0.0)	6 (0.0)	32, 13
(*Butorides virescens*)	1Y	6 (0.0)	6 (0.2)	1 (1.0)	0 (—)	3 (0.0)	6 (0.0)	22, 2
Black-crowned Night-Heron	AD	7 (0.6)	5 (1.0)	5 (0.2)	6 (0.0)	7 (0.0)	7 (0.1)	37, 11
(*Nycticorax nycticorax*)	1Y	2 (0.0)	10 (0.2)	7 (0.1)	6 (0.5)	4 (0.0)	5 (0.0)	34, 6
Yellow-crowned Night-Heron	AD	4 (0.8)	6 (0.8)	0 (—)	1 (0.0)	2 (0.0)	4 (0.5)	17, 10
(*Nyctanassa violacea*)	1Y	4 (0.0)	5 (0.6)	3 (0.0)	3 (0.3)	0 (—)	2 (0.0)	17, 4
Total	AD	42 (0.6)	36 (0.9)	34 (0.2)	31 (0.0)	66 (0.0)	53 (0.2)	262, 77
	1Y	27 (0.0)	46 (0.3)	29 (0.3)	29 (0.3)	22 (0.0)	33 (0.0)	186, 31

[a] Ages are coded as AD (adult) and 1Y (first-year); see text for definitions.

[b] For first-year birds in April–June, the proportion represents those undergoing the preformative molt. First-year birds that had commenced the second prebasic molt (as indicated by the shedding of the first primary; see text) were not considered as being in active preformative molt.

[c] The total column includes the overall specimen sample and the sample collected in active molt.

from populations with boreal breeding and molt cycles. For each specimen, we assigned age and sex based on plumage and information on the specimen label. Birds were aged as either ‘‘first-year’’ (in their calendar year of hatching or through June of the following year) or ‘‘adult’’ (at least 1 year older than first-year) through examination of plumage, shape of the outer primaries and rectrices, and presence or absence of replacement patterns among the secondaries and primaries (Palmer 1962, Cramp 1977, Baker 1993; specimen examination by PP). First-year birds do not replace juvenal primaries, whereas adults often show wear patterns indicating gradual replacement. Juvenal outer primaries and rectrices are narrower and more pointed than those of adults, and body plumage and wing coverts of darker-plumaged herons show age-specific differences in color patterns. Individuals that showed equivocal or conflicting characters ($n = 19$ of 467, particularly among white-plumaged egrets) were excluded from the sample. Sex designations reported on specimen labels—presumably based on internal examination—were assumed to be correct.

We categorized specimens as actively molting if contour feathers (excluding ornamental plumes) or flight feathers were growing. Contour feathers throughout all body tracts were carefully lifted and examined for pins or developing feathers (cf. Johnson 1963). In specimens not actively molting when collected ($n = 340$), occurrence and extent of contour-feather molts were assessed by examining the proportion of replaced feathers that were markedly fresher than juvenal or basic feathers, considering the duration of the previous prebasic molt and temporal period since its completion. Fewer than five new contour feathers were assumed to represent adventitious replacement (e.g., after accidental loss) rather than molt. Although flight-feather replacement patterns can be complicated in herons (cf. Shugart and Rohwer 1996), flight-feather molt can be an accurate temporal marker for prebasic molt; e.g., we considered the second prebasic molt to have commenced

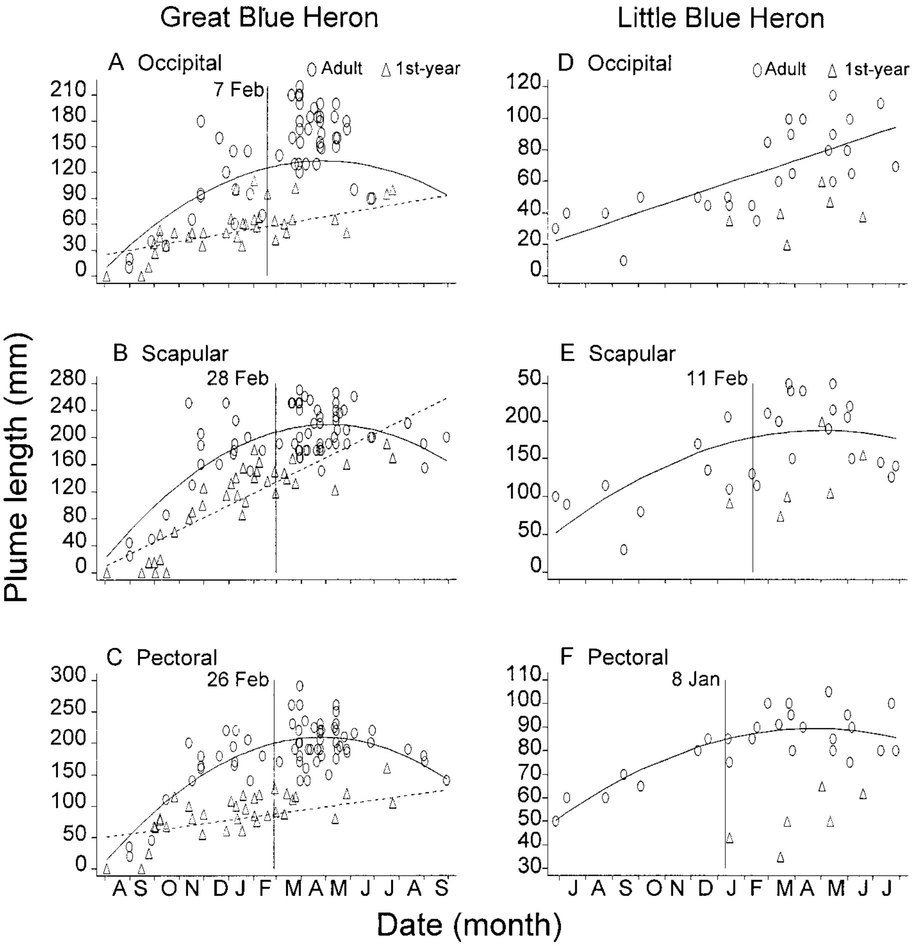

FIG. 1. Occipital, scapular, and pectoral plume lengths by month (Julian date) and age in Great Blue and Little Blue herons, indicating slow rate of growth and lack of replacement during winter and spring. Curvilinear regression lines (adult herons) are shown where quadratic terms were significant (see text); otherwise, linear regressions (dashed for first-year Great Blue Herons, solid for adult Little Blue Herons) are shown. Vertical lines represent the estimated date at which plumes attain full length within the population (95% of the maximum value of the fitted quadratic curves). Sample size (n = 6) for first-year Little Blue Herons was insufficient for meaningful regression analysis.

when the innermost juvenal primary had been shed.

To assess the growth rate of ornamental feathers at the population level, we measured—from insertion to tip—the longest occipital, scapular, and pectoral plumes in adult Great Blue and Little Blue herons. Specimens on which the longest plume appeared to be missing or broken were excluded. Growth of ornamental plumes was estimated using linear and non-linear regression of plume length against Julian date and a quadratic date term (date^2), respectively, the latter to estimate the curvilinear rate of growth (see Seber and Wild 2003 for use of quadratic terms in regression). Julian dates were based on a starting point of 1 June to include the subsequent prebasic molt, and an ending point of 30 September to include the prior prebasic molt, thus ranging from 1 to 487 (15 months). We estimated the completion of plume development as the date by which the fitted quadratic curve had reached 95% of its maximum value (see Fig. 1). Unless specified, results of non-linear regression are reported when the quadratic term was significant; otherwise, results of linear regressions are reported. Sex-specific differences in plume lengths were assessed using Analysis of Variance (ANOVA). Statistics were performed using the program Stata (Stata Corporation 1997).

Molt and plumage terminology follows Humphrey and Parkes (1959) except for that of the first molt cycle, in which we use the terms ''formative plumage'' (in lieu of the traditional term ''first basic plumage'') and ''preformative molt'' (in lieu of ''first prebasic molt'') following Howell et al. (2003).

RESULTS

Molts in herons and egrets.—Of 448 aged individuals, 186 were first-year birds and 262 were adults (Table 1). Among adults, active prebasic molt occurred in birds collected from 15 June to 23 November ($n = 77$). Among first-year birds, active preformative molt occurred from 14 September to 24 February ($n = 29$). The second prebasic molt had commenced in 12 of 33 birds collected between 28 April and 30 June, the date after which first-year birds were reclassified as adults (Table 1). No active contour-feather molt was detected in 97 adults collected in January–April (Table 1), and no evidence of partial prealternate molts was detected in 70 adults collected between April and the onset of the subsequent prebasic molt (May–August).

Fourteen adults (7 Great Blue Herons, 1 Snowy Egret, 2 Reddish Egrets, 3 Little Blue Herons, and 1 Cattle Egret) were in the process of replacing ornamental plumes when collected. In all 14 specimens, short new plumes were in pin or were emerging adjacent to retained old plumes. These specimens were collected between 17 August and 23 November during the later stages of active prebasic flight-feather and contour-feather molt. On the Cattle Egret, the older plumes were tawny and the newer plumes were white.

In first-year birds, the preformative molt showed substantial variation in extent. In 29 individuals collected between 1 March and commencement of the second prebasic molt, the extent of replacement ranged from most feathers of the head and neck and a few scapulars (Great Blue Heron MVZ15554), to all or nearly all body feathers, all lesser and median coverts, five proximal secondaries (including the tertials), and five medial rectrices (Green Heron CAS24684). Ornamental plumes were developed as part of this molt, as evidenced in 91.9% of 86 first-year individuals collected between November and May, before the onset of the second prebasic molt. These formative plumes were similar in form to those of adults but were shorter in length (Fig. 1; see below). The lack of a prealternate molt during first and later molt cycles and the timing and extent of preformative molt were similar among all 10 taxa (Table 1).

Ornamental plume lengths in Great Blue and Little Blue herons.—Our data indicate that the ornamental plumes of adult Great Blue and Little Blue herons emerged in September or October during the prebasic molt (see above) and continued to grow through January or February, after which growth ceased (Fig. 1). For all three plume types of Great Blue Heron ($n = 47$–58; Fig. 1A–C), and for scapular ($n = 22$; Fig. 1E) and pectoral ($n = 26$; Fig. 1F) plumes of Little Blue Heron, growth rates were negatively curvilinear ($t < -2.79$, $P < 0.008$ for four analyses, and $t = -0.201$, $P = 0.056$ for scapular plume length in Little Blue Heron), indicating decelerated or arrested growth during the summer and early fall. Estimated dates for attainment of full plume length varied from 8 January to 28 February (Fig. 1), and were earlier in Little Blue Heron (8 January to 11 February) than in Great Blue Heron (17–28 February). Plume length of adults appeared to shorten during June–October, presumably due to wear. Growth of occipital plumes in adult Little Blue Herons was linear ($t = 5.48$, $P < 0.001$; $n = 26$) but not curvilinear ($t = -0.063$, $P = 0.54$) with respect to date, suggesting continued growth through the summer (Fig. 1D). There was no indication that plumes in either species were replaced at any time other than during the prebasic molt (Fig. 1).

In first-year Great Blue Herons, for which sample size ($n = 35$) was sufficient to perform regression analyses, plume lengths showed significant linear trends for all three plume types ($t > 4.03$, $P < 0.001$; Fig. 1A–C), but non-significant curvilinear trends in two of three types ($t > -1.20$, $P > 0.065$ for occipital and pectoral plumes; $t = 4.62$, $P < 0.001$ for scapular plumes), generally indicating continued growth of preformative plumes into the spring.

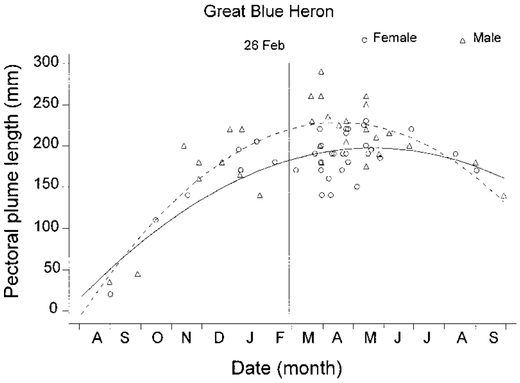

FIG. 2. Pectoral plume length by month for male and female Great Blue Herons, showing greater plume lengths of males (dashed curvilinear regression line) than females (solid line).

In adults, full-grown plumes (on dates following those on which the fitted quadratic curve had reached 95% of its maximum value; Fig. 1) were longer in males than in females and this comparison was significant for all three plume types of Great Blue Heron (ANOVA: $F > 6.79$, $P < 0.013$, $n = 49–58$) and for pectoral plumes in Little Blue Heron ($F = 4.15$, $P = 0.046$, $n = 26$). For example, mean pectoral plume length of male Great Blue Herons from 26 February to 27 September (Fig. 2) was 217.8 mm (95% CI = 146–290, $n = 20$), whereas mean pectoral plume length of females was 190.3 mm (95% CI = 138–242, $n = 29$). When dates were restricted to 26 February to 15 May (before the effects of feather wear obscure sex-specific differences; see Fig. 2), mean pectoral plume length was 231.2 mm for males (95% CI = 171–291, $n = 10$) and 182.6 mm for females (95% CI = 135–231, $n = 19$).

DISCUSSION

Our results suggest that herons and egrets lack a prealternate molt, despite widespread opinion to the contrary. There was no evidence of active contour-feather replacement among 167 adults collected between January and the onset of the prebasic molt (as early as 15 June). Direct specimen examination and growth-curve data indicate that ornamental plumes emerge during the later stages of the definitive prebasic molt in August–November, grow slowly through January–February, and are kept until replaced during the next prebasic molt. A slow rate of growth has also been documented for ornamental feathers of tropicbirds (Veit and Jones 2004), indicating that such feathers may require substantial resources to produce; thus, it seems both unlikely and unnecessary that these feathers would be replaced twice per year.

Herons and egrets thus exhibit the Complex Basic Strategy of molt as defined by Howell et al. (2003), as do other species (e.g., bitterns and tiger-herons) within Ardeidae (Palmer 1962; specimen examination by PP and SNGH). We believe that ornithologists concluding that a prealternate molt existed in herons and egrets have been misled by (1) the slow growth of ornamental plumes in adults—not reaching full length or becoming apparent in the field until winter or early spring; (2) the protracted preformative molts, which usually include growth of ornamental plumes on first-year birds into the following spring; and (3) a plumage color change during spring in at least one species, the Cattle Egret.

Molt in Cattle Egret was examined by Siegfried (1971) and discussed by Telfair (1994). Siegfried's data indicated that this species may have only one molt per year and that new white ornamental plumes replaced old pigmented plumes after the breeding season; however, he did not discuss these findings in relation to molts in Ardeini. Telfair critiqued Siegfried's study and proposed a molt strategy involving a prealternate molt that included longer alternate ornamental plumes replacing shorter basic plumes. Although our sample size of Cattle Egrets was small, our study indicates only a single replacement of ornamental plumes during the prebasic molt, as in other herons and egrets. As first suggested by Humphrey and Parkes (1963) and later discussed by Telfair (1994), the ornamental plumes of Cattle Egrets appear to gain pigmentation by staining derived from the uropygial gland or topical deposition of carotenoids, rather than through replacement of plumes. Our examination of 14 adult Cattle Egret specimens supports this supposition: none showed evidence of a prealternate molt, and color saturation of the pectoral and scapular plumes generally became darker in a clinal manner (with individual variation; cf. Maddock 1989) as date of collection progressed from winter through spring.

Our study also indicates that male herons and egrets develop longer ornamental plumes, at least on average, than females. This is the first evidence for sex-specific plumage differences among North American Ardeini and suggests that longer plumes in males than in females are due to sexual-selection strategies. It is possible that these differences are greater than those we report, due to mis-sexed individuals in our sample (cf. Parkes 1989). We suggest that more comprehensive analyses or models, using a combination of all plume lengths and date on individuals of confirmed sex, may produce methods for the accurate sexing of adult herons and egrets during spring.

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