



Use of Wing Feather Loss to Examine Age-Related Molt in Oriental Storks (*Ciconia boyciana*)

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ABSTRACT

Reproduction and molt are costly processes in avian life histories. These two fitness-related traits are expected to be under one of physiological trade-offs. Age-related molt is known to be higher in young birds than that in adults presumably due to the cost of reproduction in adults. The present study partially replicated a previous study using a non-invasive method of seasonal wing feather loss instead of capture-inspection for molting progress in oriental storks (*Ciconia boyciana*). We first examined characteristics of the known six wing feather types (i.e., primaries [P], primary coverts [PC], secondaries [S], secondary coverts [SC], and tertials [T]) from two specimens with four wings. Results were utilized as references for further investigation. We then collected a total of 3,807 wing feathers shedded by 61 captive storks for one year and classified them into six wing feather types based on the reference with structures of vane (i.e., how asymmetrical) and calamus (i.e., how rigidly attached to skin) of wing feathers. Our results indicated that annual losses of all six-type wing feathers decreased with increasing ages, ranging from 29% to 58% for PC, alula, SC, P, S, and T in order. Our results were also comparable to those of a former study, suggesting that the pattern of age-specific molt might be associated with the cost of reproduction in adults. However, juveniles might shed more wing feathers with low quality formed during the previous development stage than older birds.

Keywords: Age-related molt, *Ciconia boyciana*, Cost of reproduction, Life history, Trade-off

Introduction

Life histories of birds include costly processes such as reproduction, molt, and/or migration (e.g., birds breeding in temperate and polar zones), determining their annual life cycles presumably with minimum of energetic

stress (Bridge, 2011; Cornelius *et al.*, 2011; Payne, 1972). Replacement of old and worn feathers through molting processes plays a crucial role in arranging functions for future events such as flights, thermoregulation, species recognition, sexual display, and/or camouflage (Amadon, 1966). In a long-term perspective, climate change such as global warming may influence avian phenological processes with respect to reproduction and migration schedules, including feather molt through various physiological mechanisms (Kiat *et al.*, 2019a; 2019b). However, empirical data and knowledge on avian molt of various species and contexts are relatively insufficient due to limitations

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in examining variations of avian molt along their life cycles compared to studies of other life history traits (e.g., reproduction) of many species.

The evolution of organisms encompasses the optimization of resource allocation strategies with minimization of fitness-related costs (Roff, 1992; Stearns, 1992). Variation in resource allocation can be shaped by trade-offs among several life history traits, including growth versus molt (Kiat & Izhaki, 2016), growth versus reproduction (Kiat & Sapir, 2018), reproduction versus molt (Svensson & Nilsson, 1997), molt versus migration (Gordo, 2007), and life history contrasts between residents and migrants in a given environment (Kiat *et al.*, 2019a). To date, results of many studies support the adaptive significance of resource allocations where investing too many resources into a certain trait or overlapping two traits are likely to cause current and/or future fitness-related costs. Therefore, the differences between post-juvenile's and adult's molt followed by distinction in juvenile-adult feather quality can be explained by resource allocation under trade-offs among growth, reproduction, and molt of birds along their developmental stages (Kiat & Izhaki, 2016; 2018).

Hall and Gwinner (1987) has discovered that the degree of age-related molt is higher in young birds than in adults of white storks (*Ciconia ciconia*) during the spring-summer period probably due to the cost of overlapping or upcoming reproduction and migration. Adult storks with relatively lighter molt breed at the similar time window of molt and migrate longer distance than juvenile storks with low costs of reproduction and/or migration. However, little is known about characteristics of wing feathers and patterns of oriental storks (*Ciconia boyciana*) known to be closely related to white storks (Elliott *et al.*, 2020). The purpose of this study was to determine characteristics of black-colored wing feathers' structures in oriental storks. Results from known wing feathers of two specimens were utilized as references. We then examined variation in age-related wing molt using collection and classification of wing feather losses in captivity. We also discussed molt patterns of oriental storks (i.e., juvenile vs. adult) in a life-history perspective with resource allocation.

Materials and Methods

Study site and species

The present study was conducted in the breeding facility of Ecological Institute for Oriental Stork, Korea National University of Education (KNUE), Cheongju, Republic of Korea (36°36'15" N, 127°21'33" E). Two breeding facilities in Cheongju (KNUE) and Yesan Oriental Stork Park have pursued captive propagation to recover extirpated species in Republic of Korea through reintroduction and habitat management since 1996 (Park & Cheong, 2002; Park *et al.*, 2011). The oriental stork as a large soar-

ing bird is known to exhibit monogamous mating with a long-term pair bond in which both sexes incubate and provide chicks with post-hatching care throughout the spring-summer breeding season (Cheong, 2005; Elliot *et al.*, 2020; Yoon *et al.*, 2015a). Oriental storks in the wild build large nests (diameter of 2 m) typically in 10-15 m tall trees (range, 3-30 m) that are often dead trees with good visibility (Elliott *et al.*, 2020). Parents have solitary breeding with strong territoriality. They raise nidicolous young prior to independence (Starck & Ricklefs, 1998). Storks seem to be at maturity when they become three years old after hatching (i.e., in 2.5 years after fledging in June; J. Yoon, *personal observation*). They start to display courtship and nest-building behaviors in December (Yoon *et al.*, 2015a; 2015b). Thus, we defined the age class of oriental storks into juvenile (hatch year to 3rd year) and adult (after 3rd year).

The oriental stork is internationally listed as an endangered species due to its habitat loss and overhunting in the past. It currently breeds only in Russia and partially in China (BirdLife International, 2018). To date, there are 118 captive storks managed in facilities. Eighty-six storks have been released into recovery sites of Yesan County, Republic of Korea (36°36'32" N, 126°48'05" E) since 2015. Yet, few researchers have extensively conducted a comparative study on life history traits such as reproduction, molt, and/or migration of wild (e.g., migrants in Russia or China) versus reintroduced (e.g., probably residents or short-distance migrants) oriental storks in Republic of Korea and Japan (reintroduction started since 2005).

Measurement of referenced wing feathers

We first collected wing feathers from two adult stork specimens with four wings (n=4) as references for further classification. We then measured six types of wing feathers: alula (A) (1-4), primaries (P) (1-11), primary coverts (PC) (1-11), secondaries (S) (1-22), secondary coverts (SC) (1-22), and tertials (T) (1-7). Permission for feather use from specimens was acquired from Cultural Heritage Administration previously. Characteristics of wing feathers included two portions: vane and calamus structures (Fig. 1). Vane structure referred to the degree of asymmetry with differences between trailing and leading edge in width (mm) and angle (degrees to the shaft) at the mid-point of vane. Calamus structure denoted the degree of rigid attachment to the wing skin including length (mm) of total calamus, skin level to inferior/superior umbilicus, percent skin level, and calamus diameter. Here, these two structural features were selected because they tended to be well shaped with less abrasion in old, worn, and shedded feathers in captivity (J. Yoon, *personal observation*). We used calipers and ImageJ software (Image Processing and Analysis in Java version 1.8.0.; <https://imagej.nih>).

gov/ij) for a variety of measurements (Fig. 1).

Collection and classification of shedded wing feathers

To examine annual and seasonal age-related molt patterns (October 2015 to September 2016), 61 captive oriental storks were separately kept in five cages: one-year-old (6 individuals [indv.]), 2-year-old (16 indv.), 4-year-old (6 indv.), 5-year-old (15 indv.), and 6-year-old (18 indv.). Here, age was defined as the age when the collection of feather losses (Rohwer & Brom, 2012) started. One-year old was referred to hatch year. Shedded wing feathers were collected in each cage twice a week to prevent any damages and stored by each month where cage fences were dense enough to keep shed wing feathers for

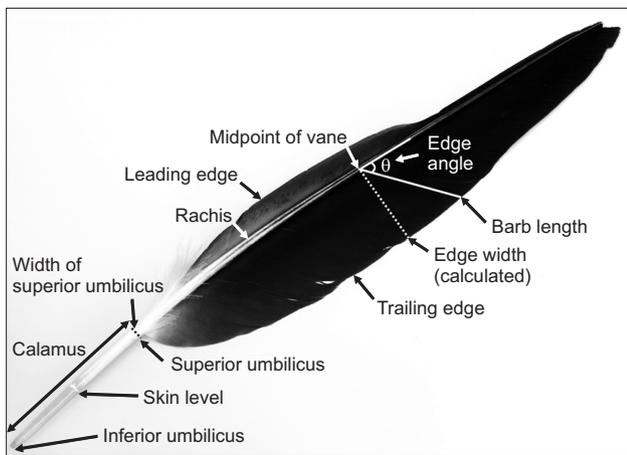


Fig. 1. Terminology of black-colored wing feather structure. The left-bottom part shows measurements of calamus structure and the right-upper portion indicates measurements of vane structure.

a short time of period. Collected feathers were washed and dried to make normal shape, especially vanes, prior to measuring and classifying into six types of wing feathers.

Statistical analyses

We used a generalized mixed model to analyze structural characteristics of wing feathers as references, controlling for each individual as well as changes in wing feather loss as a function of age, feather type, and two-way interaction. We then used a principal component analysis and Pearson’s correlation to document shapes of six wing feather types (i.e., the degree of asymmetry in vane and rigid attachment in calamus) using PC composite scores of vanes (6 variables) and calamus (5 variables) measures (e.g., eigenvalue greater than 1). All statistical analyses were performed with SPSS for Windows, Version 16 (SPSS Inc., Chicago, IL, USA). We did not need to transform any variables to meet model assumptions.

Results

Averages of all wing feathers (i.e., vane and calamus structures) with 5 known classes and within-class orders (i.e., 77 types) from two specimens were calculated as references (Supplementary Table 1). First, PC score for vane structure was representative for the degree of vane asymmetry (eigenvalue=3.29). PC score increased with decreasing vane asymmetry found in the trailing (wider, more gradual)-leading (narrower, steeper) edge of vanes (Fig. 2A). Here, the degree of vane asymmetry ranged from P, PC, A, SC, S, and T in order. Second, PC score for calamus structure was representative for the degree of rigid attachment of feathers to the wing skin (eigenvalue=4.39). PC score increased as the calamus was longer and thicker with deeper skin level (Fig. 2B). Here, the degree of cala-

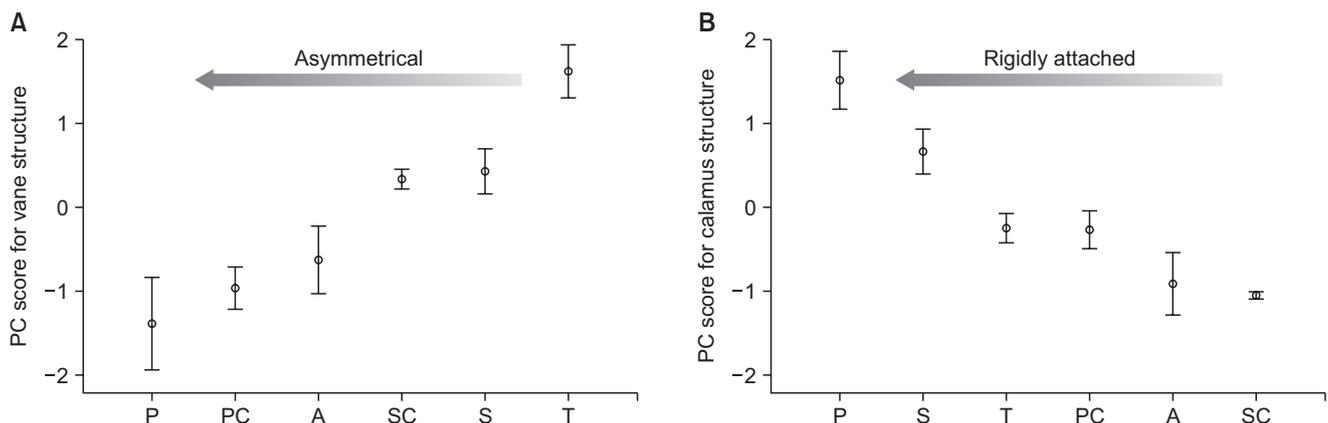


Fig. 2. Structural patterns of known wing feathers of oriental storks with 95% confidence intervals of PC scores for (A) vane and (B) calamus structures (n=77). X-axis denotes each part of wing feathers. P, primaries; PC, primary coverts; A, alula; SC, secondary coverts; S, secondaries; T, tertials.

mus rigidity ranged from P, S, T, PC, A, and SC in order.

All wing feathers ($n=3,807$) collected for a year were classified into six types. As shown in Fig. 3, seasonal feather loss (i.e., per capita, the number of feather losses divided by the number of individuals in each cage) appeared to start earlier and become seasonally more expanded in juvenile storks (i.e., hatch year to 2nd year) than adult storks (i.e., after 3rd year) with increasing age. The annual wing feather loss differed by feather type and age (mixed model: $F_{5,18}=3.33$, $P=0.03$; $F_{1,18}=7.80$, $P=0.01$; $F_{5,18}=0.40$, $P=0.84$; Fig. 4). Specifically, the proportion of wing feather losses varied for the six types: A (31%), P (41%), PC (29%), S (43%), SC (34%), and T (59%). The percentage of all feather losses significantly decreased with age (slope= -4.45 ± 1.96).

Discussion

We documented that the degree of wing feather molt in young birds was at a higher rate than that in adults presumably due to the cost of reproduction in adults of oriental storks. The present study partially replicated the study of Hall and Gwinner (1987) for white storks using a

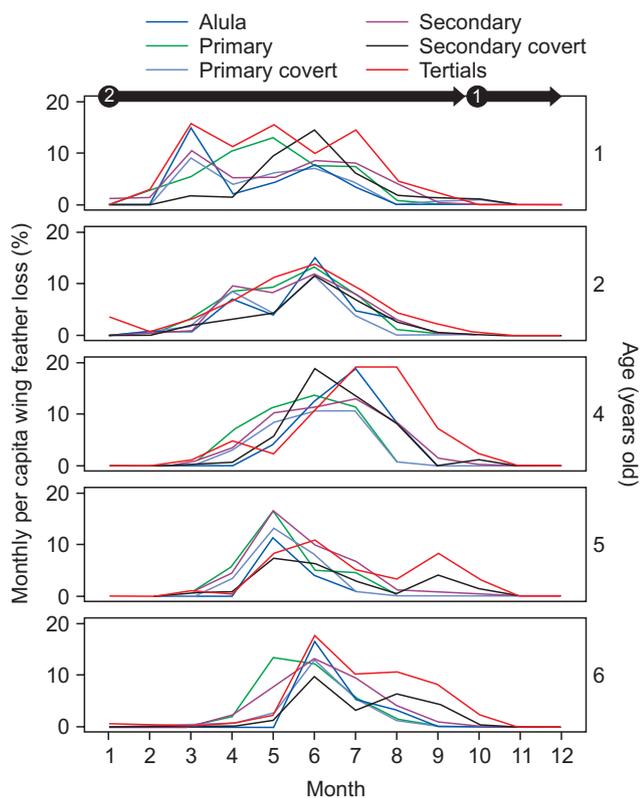


Fig. 3. Seasonal variation in per capita wing feather loss (%) of oriental storks in relation to feather type and age. Circled numbers denote a series of feather collection (i.e., October 2015 to September 2016).

non-invasive method based on annual wing feather loss for molting inspection (Rohwer & Brom, 2012). Our results indicated that wing feather loss annually decreased with increasing age (Fig. 4) where juveniles (i.e., hatch year to 3rd year) tended to molt earlier and temporally elongated compared to adults (i.e., after 3rd year) with respect to seasonal variation in wing feather molt (Fig. 3). Our results were comparable to those of a previous study (Hall & Gwinner, 1987), suggesting that differences in age-specific molt found in oriental storks might be associated with the cost of reproduction in adults.

In a life history perspective, resource allocation strategies are necessary under various trade-offs among self-maintenance (e.g., growth and molt), reproduction, and other demands depending upon the ontogenetic stage of early life in birds (Roff, 1992; Stearns, 1992). Here, fitness-related costs of molt-breeding overlap were well studied for adults through experimental approaches (e.g., enlarged brood size or simulated molt) to increase the cost of reproduction, specifically in pied flycatchers (*Ficedula hypoleuca*) and blue tits (*Cyanistes caeruleus*). Parents with enlarged broods tended to delay molting compared to those with control broods, where the degree of molt was lighter and briefer in males and young birds than in females or old birds during the nestling period (Siikamäki *et al.*, 1994; Svensson & Nilsson, 1997). Also, molt-breeding overlap simulated by removing wing feathers is known to lower parents' body condition, recruitment rate, and return rate to next year, resulting in current and/or future fitness costs (Hemborg & Lundberg, 1998).

Compared to costs of molt-breeding overlap found in adults, juveniles might need another resource allocation strategy under a trade-off between growth and molt at the early developmental stage after hatching. The amount

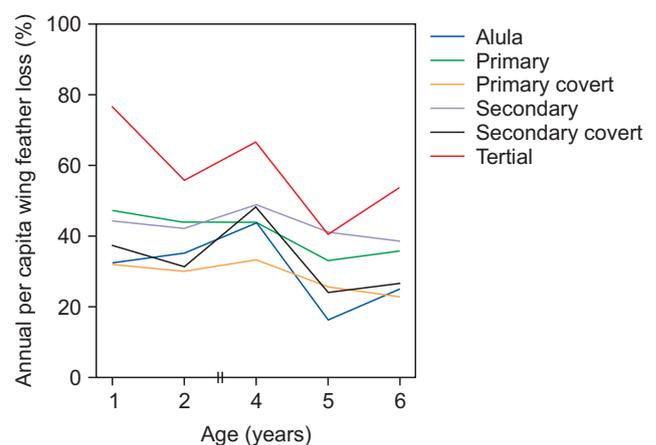


Fig. 4. Annually accumulated per capita wing feather loss (%) of oriental storks ($n=61$) as a function of age and feather type.

of post-juvenile molt can be either partial or complete (Kiat & Izhaki, 2016). Juveniles should favor the former strategy under high costs of survival, while others should allocate limited energetic resources into not only development, but also molt simultaneously. Furthermore, juvenile feathers can also exhibit relatively lower quality in feather length, mass, and/or melanization measurements compared to feathers of adults (Kiat & Sapir, 2018). The amount of nest-grown feathers is likely to be replaced depending on the timing of developmental completion. Therefore, patterns of age-related wing molt found in this study might be partial under two different trade-offs (i.e., growth-molt-breeding) in the puberty-maturity spectrum (i.e., juvenile to adult stages) of oriental storks.

Prior to 1950s, the distribution and life histories of oriental storks might be continuous from Russia to China, Korean Peninsula, and Japan, meaning that their life forms were likely to range from long-distance migrants towards the most northern breeding sites to short-distance migrants or residents towards the most southern breeding areas (e.g., Republic of Korea and Japan) along the latitudinal gradient. Currently, the northern population lives as long-distance migrants, while the recently establishing populations from reintroduced storks in Korea and Japan seem to live as residents because they lack the regular migratory behavior (J. Yoon, *personal observation*). It is still unknown whether migratory and released storks exhibit distinct life history traits shaped by various trade-offs among growth, molt, and reproduction at the most northern and southern parts of their distribution (Kiat *et al.*, 2019a; Wingfield, 2008). Although age-related wing feather loss is found at low-intermediate rates, future study should investigate the degree of molt-breeding overlap and its fitness-related costs of northern and newly establishing southern populations of oriental storks.

Conflict of Interest

The authors declare that they have no competing interests.

Acknowledgments

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Supplementary Table 1. Measures of known wing feathers (six classes) of two oriental storks
(n=4, left-right wing feathers included)

Class	Order*	Vane structure						Calamus structure				
		TEW	LEW	DEW	TEA	LEA	DEA	CAL	SL-IU	SL-SU	%SL	SUD
Alula	1	2.25	0.70	1.55	40.32	24.06	16.25	25.63	25.63	0.00	100	4.20
	2	2.18	0.98	1.20	41.39	28.87	12.52	24.89	24.89	0.00	100	4.08
	3	2.26	1.15	1.11	47.00	34.95	12.05	20.68	20.68	0.00	100	3.40
	4	2.13	1.15	0.98	53.09	38.94	14.15	13.92	13.92	0.00	100	2.69
Primary	1	3.22	1.50	1.72	48.70	36.56	12.14	63.12	40.90	19.82	65	6.22
	2	3.58	1.43	2.15	49.85	36.47	13.38	65.00	44.11	20.89	68	6.59
	3	3.88	1.43	2.44	48.92	36.35	12.57	66.66	44.49	22.17	67	6.83
	4	3.96	1.27	2.69	48.63	35.10	13.53	67.85	46.57	21.28	69	6.95
	5	4.53	1.04	3.50	46.29	28.35	17.94	81.24	51.24	29.13	63	7.93
	6	4.26	0.64	3.62	44.12	18.00	26.13	93.09	51.39	41.70	55	8.68
	7	3.77	0.61	3.16	43.96	16.77	27.19	97.38	59.45	37.94	61	8.65
	8	3.46	0.59	2.87	40.02	13.99	26.03	88.17	59.67	28.50	68	8.68
	9	2.95	0.40	2.55	38.97	9.51	29.47	85.04	57.03	28.01	67	7.85
	10	2.85	0.37	2.48	40.06	9.18	30.88	82.52	59.37	23.15	72	7.48
	11	2.53	0.35	2.18	37.59	10.49	27.10	59.71	43.25	16.46	73	6.92
Primary covert	1	2.03	1.24	0.79	52.48	40.08	12.39	25.00	25.00	0.00	100	2.86
	2	1.93	1.17	0.76	52.31	37.85	14.46	30.85	30.85	0.00	100	3.30
	3	2.06	1.18	0.89	55.99	35.33	20.66	37.47	37.47	0.00	100	3.92
	4	2.14	1.22	0.92	55.21	34.13	21.08	40.98	40.69	0.29	99	4.10
	5	2.21	1.31	0.89	54.59	35.33	19.27	45.21	43.76	1.45	97	4.47
	6	2.32	1.27	1.04	53.99	35.46	18.52	49.06	47.55	1.51	97	5.05
	7	2.38	1.23	1.15	52.93	37.85	15.07	53.03	52.13	0.90	98	4.96
	8	2.33	1.19	1.13	52.65	34.25	18.40	49.47	47.77	1.70	97	5.05
	9	2.22	1.01	1.21	51.01	30.68	20.33	47.01	47.01	0.00	100	4.78
	10	2.06	0.79	1.26	50.03	27.11	22.92	43.20	43.20	0.00	100	4.51
	11	1.65	0.49	1.17	44.62	20.51	24.11	34.49	34.49	0.00	100	4.17
Secondary	1	3.23	1.50	1.73	51.77	37.46	14.31	55.25	36.57	18.68	66	5.91
	2	3.53	1.71	1.83	53.22	41.82	11.41	63.01	39.98	23.03	64	5.81
	3	3.41	1.73	1.69	53.79	43.36	10.43	64.95	39.71	25.24	61	5.56
	4	3.36	1.70	1.66	53.74	42.92	10.82	60.69	39.11	21.59	65	5.68

Class	Order*	Vane structure						Calamus structure				
		TEW	LEW	DEW	TEA	LEA	DEA	CAL	SL-IU	SL-SU	%SL	SUD
	5	3.28	1.78	1.49	52.22	41.77	10.45	59.80	37.26	22.54	62	5.66
	6	3.40	1.83	1.57	53.02	42.01	11.01	62.84	37.63	25.21	60	5.80
	7	3.28	1.76	1.51	51.39	41.76	9.63	63.52	39.28	24.24	62	5.39
	8	3.33	1.87	1.46	52.52	42.30	10.22	64.61	36.84	27.77	57	5.31
	9	3.33	1.86	1.47	52.74	42.00	10.74	64.13	37.17	26.96	58	5.46
	10	3.41	1.90	1.51	54.09	42.89	11.21	64.74	36.94	27.80	57	5.46
	11	3.43	2.05	1.38	55.32	43.74	11.58	65.70	37.36	28.34	57	5.56
	12	3.49	2.09	1.40	51.87	44.54	7.34	63.82	36.67	27.15	58	5.63
	13	3.76	2.32	1.43	54.87	44.31	10.56	63.90	37.07	26.83	58	5.67
	14	3.85	2.40	1.45	54.95	42.84	12.11	65.66	37.07	28.59	57	5.79
	15	3.97	2.47	1.50	53.83	44.15	9.68	65.01	38.25	26.77	60	5.56
	16	4.22	2.56	1.66	55.03	42.97	12.06	53.95	36.03	17.92	67	5.68
	17	4.14	2.76	1.38	51.83	42.23	9.59	53.12	34.35	19.54	65	5.69
	18	3.96	3.16	0.80	52.04	42.53	9.51	52.71	32.07	20.64	61	5.60
	19	3.68	3.29	0.40	45.99	40.23	5.76	45.48	29.11	16.37	64	5.08
	20	3.28	3.26	0.01	41.18	40.20	0.98	35.97	26.14	9.84	74	4.38
	21	2.91	2.88	0.04	40.45	35.83	4.62	24.60	22.21	2.39	92	3.63
	22	2.13	2.02	0.11	40.60	38.44	2.15	12.30	10.94	1.36	92	2.25
Secondary	1	2.24	1.59	0.65	57.66	42.45	15.20	23.35	23.35	0.00	100	2.91
covert	2	2.38	1.83	0.54	56.94	43.97	12.97	25.00	25.00	0.00	100	2.97
	3	2.32	2.01	0.31	56.85	45.85	11.00	23.52	23.52	0.00	100	2.99
	4	2.24	2.03	0.20	56.20	47.69	8.51	22.91	22.91	0.00	100	2.74
	5	2.35	1.96	0.39	55.43	44.69	10.74	21.98	21.61	0.37	98	2.48
	6	2.24	2.06	0.18	53.92	45.16	8.76	21.02	20.45	0.56	97	2.76
	7	2.20	1.98	0.22	54.66	45.30	9.37	20.57	20.35	0.23	99	2.57
	8	2.31	2.07	0.24	56.07	47.14	8.92	20.52	20.52	0.00	100	2.61
	9	2.39	1.92	0.47	55.69	45.52	10.17	19.41	19.41	0.00	100	2.55
	10	2.36	1.99	0.37	54.74	45.56	9.18	20.58	20.58	0.00	100	2.76
	11	2.38	2.07	0.32	52.97	45.48	7.49	20.64	20.64	0.00	100	2.64
	12	2.36	1.99	0.37	54.48	44.26	10.22	19.32	19.32	0.00	100	2.55
	13	2.28	2.11	0.17	49.42	44.45	4.98	19.36	19.36	0.00	100	2.48
	14	2.24	2.14	0.11	53.35	45.01	8.34	18.79	18.79	0.00	100	2.61
	15	2.38	2.08	0.30	57.73	43.93	13.80	20.24	20.24	0.00	100	2.65
	16	2.35	2.03	0.32	56.65	44.40	12.25	19.66	19.44	0.22	99	2.49

Class	Order*	Vane structure						Calamus structure				
		TEW	LEW	DEW	TEA	LEA	DEA	CAL	SL-IU	SL-SU	%SL	SUD
	17	2.29	2.08	0.21	54.98	45.33	9.65	19.48	19.48	0.00	100	2.56
	18	2.45	2.05	0.40	52.86	44.98	7.88	19.90	19.62	0.28	98	2.63
	19	2.45	2.04	0.41	54.33	44.01	10.32	22.59	22.59	0.00	100	2.83
	20	2.48	2.05	0.43	52.36	42.79	9.58	20.42	20.10	0.32	98	2.98
	21	2.40	2.07	0.33	49.55	42.86	6.69	19.14	19.14	0.00	100	2.89
	22	2.06	1.82	0.24	40.45	37.32	3.13	10.51	10.51	0.00	100	2.13
Tertial	1	2.99	2.55	0.45	40.06	37.06	3.00	32.79	30.43	2.36	93	4.06
	2	3.20	2.81	0.39	41.14	37.20	3.94	35.79	33.12	2.68	93	4.32
	3	3.52	3.24	0.28	42.14	42.85	-0.71	40.29	32.83	7.47	82	5.03
	4	3.23	3.21	0.02	42.54	42.14	0.40	37.53	31.14	6.39	83	4.75
	5	3.08	3.14	-0.05	43.55	45.32	-1.76	38.68	34.56	4.12	89	5.02
	6	3.13	2.93	0.20	40.82	38.20	2.62	37.95	33.29	4.67	88	4.59
	7	3.14	2.84	0.30	45.41	39.90	5.51	32.62	31.28	1.34	96	4.10

Numbers denote means of measurements (Fig. 1).

TEW, trailing edge width (mm); LEW, leading edge width (mm); DEW, TEW-LEW (mm); TEA, trailing edge angle (degree); LEA, leading edge angle (degree); DEA, TEA-LEA (degree); CAL, calamus length (mm); SL-IU, length between skin level and inferior umbilicus (mm); SL-SU, length between skin level and superior umbilicus (mm); %SL, proportional length of SL-IU to calamus length (%); SUD, diameter at superior umbilicus (mm).

*Order (feather numbers): alula (4 types), primaries (11), primary coverts (11), secondaries (22), secondary coverts (22), and tertials (7).