



Moult in the Stripe-throated Bulbul, *Pycnonotus finlaysoni*: Sexual Differences and Timing

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ABSTRACT

Moult of wing feathers in passerine birds occurs annually to maintain flight abilities. This process is costly due to the high energy requirements involved in the synthesis of new feathers. This study presents basic information about the moulting of primaries and secondaries in the adult Stripe-throated Bulbul (*Pycnonotus finlaysoni*), a sexually monomorphic passerine, living in the seasonal tropical forests of northern Thailand. Specifically, we examined the moult differences between males and females. The moult season began in early June and lasted until mid November (2009). The primary moult began approximately 20 days before the secondary moult. Our comparative analysis of the moult process between the sexes showed that males started to moult earlier than females for both primary and secondary feathers. The moult process took longer for the males than for the females with an approximate primary moult of 136 days for males ($n = 11$) and 118 days for females ($n = 16$), and a secondary moult of 114 days and 101 days for males ($n = 11$) and females ($n = 16$), respectively. This is probably because of a sexual bias in breeding time investment. Males are involved earlier in the breeding process e.g. singing and establishing territory. Females have more responsibility later in the cycle e.g. incubating eggs and nestling care.

Keywords: moult, passerine, seasonal tropical forest, wing feathers

1. INTRODUCTION

Moulting in birds is the process of feather renewal whereby old feathers are pushed out and replaced by new feathers that are generated from the same feather follicle [1]. Feathers are nonpermanent structures that become worn with age, impairing flight efficiency. Feather abrasion may be caused by several factors including

fighting, rubbing against vegetation or other objects, keratin degradation by photochemical processes, and degradation by ecto-parasites, bacteria and fungi [2]. Thus, birds must renew their feathers to maintain flight efficiency, a process which, among smaller birds, is undertaken at least once per year [3]. Moult is costly, as the synthesis of new

feathers requires large amounts of energy and protein [4, 5, 6].

The moult period of each species varies according to their specific energy requirements, and, birds do not usually moult during the same period as other energetically-costly processes such as breeding or migration [7]. Most resident birds usually moult after their breeding season [8, 9], while migrants usually moult either before or after migration depending on the species or population [10, 11, 12]. Factors such as food availability need to be sufficient to sustain the energy-consuming process of moult [5, 7, 13]. Thus, the extent of the moult can be influenced by annual variations in food supply [14]. An extended period of parental care involvement during the breeding season can influence the timing of the moult. This is often seen in many passerines in which the females of some species tend to provide more continuous parental care and for a longer time and therefore moult later than the males [3, 15].

Asiatic bulbuls are non-migratory passerines and widely distributed throughout South-East Asia. They are considered important seed dispersers that have a significant impact on patterns of seed dispersal in the Asian region [16]. However, little is known about the patterns of moult in this group. The moult process across species that has been reported varies in term of duration and timing e.g. Yellow-vented Bulbuls (*Pycnonotus goiavier*) moult between April and September and feather regeneration takes ~120 days [8], whereas Grey-eyed Bulbul (*Iole propinqua*) feather regeneration takes ~126 days from June to September [9]. However, sexual differences in moult duration within a species has not been described in most species of this group.

This study describes the timing and progression of flight feathers moult of the

Stripe-throated Bulbul (Aves: Passeriformes, Fam. Pycnonotidae, *Pycnonotus finlaysoni*) in its natural habitat in the seasonal tropical forests of northern Thailand. It is a resident of Thailand [17, 18], and usually feeds on plant foods (e.g. leaves, ripe or unripe fruit and nectar) and, very rarely, animal foods (e.g. insects and small lizards) [19, 20]. Our study focused on the moult of the flight feather of the wings, the primaries and secondaries using quantitative methods to assess the timing and duration of the moult. We tested whether there were differences in moult progression between the sexes.

2. MATERIALS AND METHODS

2.1 Study Site

This study was conducted near Chiang Dao Wildlife Research Station (19°21' N, 98°55' E). The study site ranged in elevation between 400 and 700 m a.s.l. The area is typical lowland seasonal deciduous forest, most of which was secondary growth that has replaced the original teak (*Tectona grandis*) - dominated mixed deciduous forest - following several decades of logging [21, 22, 23]. Currently, the vegetation consists predominantly of several species of bamboo (Gramineae, Bambusoideae) woody climbers, and seedlings and saplings of numerous tree species [21].

The climatic data collected during this study showed three distinct seasons at our study site; a cool-dry season (November-January), a hot-dry season (February-April), and a rainy season (May-October). The first rains began in March, and lasted until October. The highest rainfall was between May and September with an average monthly rainfall of 592 mm (SE = 141.2). Minimum temperatures recorded at the study site ranged from 11.4 to 21.7 °C. The lowest minimum temperature was in January (11.4 °C). The hottest month was in April

(33.8 °C) with an average daily maximum temperatures ranged from 22.6 to 33.8 °C (SE = 3.4).

2.2 Study Species

Stripe-throated Bulbuls can be found at elevations of up to 1,300 m [17, 18], in a wide range of habitats including: orchards, secondary growth, scrub, open areas, broadleaf evergreen, mixed deciduous, and evergreen forest [18, 24, 25]. This bird feeds on a variety of fruits, together with a small amount of insects [19, 20], and moves between fruiting trees usually in small foraging flocks within the mid-storey of the forest canopy. We caught birds during multiple sessions which included 2-3 weeks

of the post-breeding season. The birds were caught using mist nets on 37 days between June and November 2009. It was also when other species (e.g. Grey-eyed Bulbul) were known to be moulting [9]. The overall effort amounted to 20,350 m-hours of netting. We used 3 panel mist nets: 9 m and 12 m long with mesh sizes of 1.5 and 2.0 cm, respectively. The net lines were usually positioned between bushes close to fruiting trees. Standard morphometric measurements were obtained for all captured birds, including: bill, tarsus, wing, and weight (Table 1). In order to avoid resampling the same individuals, we cut a small portion of the tip of the right outer tail feather of each individual measured.

Table 1. Morphometric comparisons between male and female Stripe-throated Bulbuls at Chiang Dao Wildlife Research Station during the moult period between June and November 2009.

Measurements	Male (n = 11)		Female (n = 16)		<i>p</i> -value
	Average ± SD	range	Average ± SD	range	
Weight (g)	30.1 ± 2.8	28.2 - 32.0	29.0 ± 2.5	27.6 - 30.3	0.270
Bill (mm)	18.6 ± 0.2	18.5 - 18.8	18.5 ± 0.9	18.1 - 19.0	0.713
Tarsus (mm)	20.0 ± 0.7	19.5 - 20.5	19.8 ± 1.0	19.3 - 20.3	0.502
Wing (mm)	82.7 ± 3.7	80.3 - 85.2	80.1 ± 1.6	79.2 - 80.9	0.042

Adult Stripe-throated Bulbuls are difficult to distinguish from juveniles but their rectrices (tail feathers) and remigs (flight feathers) during and immediately following the breeding season are usually distinctively worn and faded compared to those of juveniles [9]. In addition, the presence of down feathers (usually on the head or throat), a yellow patch on the base of the beak gape, and less yellow plumage on the face are typical of juvenile plumage. Based on these characteristics, we were able to include only adult birds in this study. Post juvenile moult, including replacement of flight feathers, was observed during this study, although too few juveniles were caught to

estimate moult duration in that age-class. After measuring and scoring for moult the birds were immediately released in the same locations where they had been caught.

2.3 Sexing

Since Stripe-throated Bulbuls are sexually monomorphic, we used molecular techniques for sex identification [26, 27]. We collected approximately 10 µl of blood from the tarsus vein [27], on filter paper (Whatman®) which was kept at room temperature until DNA extraction. We obtained genomic DNA from whole blood using proteinase K and phenol-chloroform extraction [28, 29]. We performed polymerase chain reactions

(PCR) using primers P8 (5'-CTC CCA AGG ATG AGR AAY TG-3') and P2 (5'-TCT GCA TCG CTA AAT CCT TT-3') [26]. The reactions were run in a 25 μ l volume, and included 1 μ l of DNA template, 1.5 μ l of 10X PCR buffer (Bioscience), 1 μ l of 10 μ M of forward and reverse primers, 1.5 μ l of 10 μ M dNTP, 1.5 μ l of 25 mM MgCl₂, 1 μ l of *Taq* DNA polymerase (Vivantis), and 14.5 μ l of diH₂O. The PCR protocol was: 5 min at 94 °C, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 30 s, extension at 72 °C for 30 s, and a final extension step of 5 min at 72 °C. The amplified PCR products were visualized on 2% agarose gel stained with ethidium bromide using electrophoresis. Sex was determined by assessing allele sizes: 320bp and 400bp in females (double band) and 320bp (single band) in males.

2.4 Moulting

Most passerines have ten primaries, six secondaries and three tertiaries. They moult primaries descendantly (centrifugally, from inside to out), while secondaries and tertiaries moult ascendantly (centripetally, out to in). Our focus was on the primaries and secondaries. Moulting was recorded following the method described in Ginn & Melville (1983) in which each primary and secondary feather was assigned a score ranging from 0 to 5, where "0" indicates an old (unmoulted) feathers, "5" indicates new, full grown, and 1-4 indicates intervening stages. The primary score is the sum of the scores assigned for each primary feather. Based on moulting scores over time, we estimated moulting progression in terms of timing and duration for each bird [3]. We used the same procedure to calculate the progression of secondary moulting. We used a simple linear regression model

($y = ax + b$) to predict moulting progression [3]. Our estimated moulting progression is based on a small sample size, and it tends to slightly overestimate the moulting duration [9], see Underhill and Zucchini (1988) for an alternative method for estimating moulting duration with larger sample sizes [30]. The variables used in the model include: "y" is an expected moulting score, "a" is an estimated slope of the regression, "b" is a regression constant, and "x" is the number of days from the expected date for the start of the moulting. In this study, x is the number of days from 1 July when we observed the first active moulting. We performed an analysis of covariance (ANCOVA) on the regressions to test whether moulting progression differed between the sexes.

All statistical analyses were conducted using MYSTAT (Chicago, IL, U.S.A.).

Ethical note

This study was complied using the guidelines for wildlife research and study (2001) set by the Department of National Parks, Wildlife and Plant, Thailand, and was approved by the Chiang Mai University Committee.

3. RESULTS AND DISCUSSION

3.1 Morphometrics and Sexing

We caught 27 Stripe-throated bulbuls (11 males and 16 females). Morphological comparisons were not significantly different between males and females in terms of weight ($t_{1,25} = -1.129, p = 0.270$), bill length ($t_{1,25} = -0.373, p = 0.713$), and tarsus length ($t_{1,25} = -0.681, p = 0.502$). Wing length, however, differed significantly between the sexes, with males having longer wings than the females ($t_{1,25} = 12.687, p = 0.042$) (Table 2).

Table 2. Moulting scores of adult Stripe-throated Bulbuls studied at Doi Chiang Dao Wildlife Research Station, in 2009. The numbers represent primary and secondary scores of the birds caught on the day present.

Feather	Sex	Estimated Moulting Duration (days)	Starting Date	Completion Date
Primary	Male (n=11)	136	17 July	28 October
	Female (n=16)	118	9 August	3 November
Secondary	Male (n=11)	114	16 August	30 October
	Female (n=16)	101	9 August	7 November

3.2 Moulting

The first active moulting in adult males was recorded on 17 July. This male started renewing the two most inner primaries (primary score = 8), but had not yet started a secondary moulting. A male caught on 16 August was the first individual in which the moulting of secondaries was recorded (new innermost secondary, full-grown, and the rest old, secondary score = 5) when the primary moulting had proceeded as far as the 4th primary (primary score = 16). The first female observed in active primary moulting was caught on 9 August (primary score = 13), 23 days after the first actively moulting male. This female had already started moulting on the innermost secondary (score = 4); no males were caught on that day. The first male who had completed moulting, in both primaries and secondaries, was observed on 8 October. A completed moulting female was first caught on 16 October

(8 days later than the male). In this study, all adult Stripe-throated Bulbuls completed moulting no later than 4 November.

Our analysis of using simple linear regression and based on small sample sizes (n = 27) predicted that primary moulting occurred between early June and early November. Secondary moulting occurred after the onset of primary moulting which approximately began in mid-June and was completed in mid-November. Our ANCOVA test of moulting progressions showed that males commenced moulting significantly earlier and experienced a longer moulting than the females both in primaries ($F_{1,24} = 5.009, p = 0.035$), and secondaries ($F_{1,24} = 6.550, p = 0.017$). Estimated moulting progression of adult Stripe-throated Bulbuls caught during our study is shown in a scattergram qualified by 95% confidence limits (Figure 1 and Figure 2).

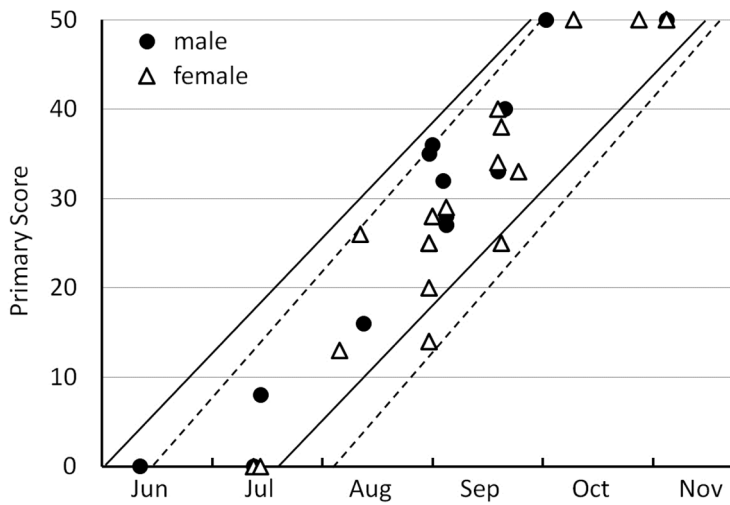


Figure 1. Scattergrams of primary progression of Stripe-throated Bulbul show moult differences between the sexes. Regression of primary moult scores against date of males and females, starting on 1 July, were $y = 0.368x + 6.206, R^2 = 0.855$ ($n = 11$), and $y = 0.425x - 2.736, R^2 = 0.720$ ($n = 16$), respectively. The lines, solid lines (males) and dash lines (females), indicate 95% confidence limits of each sex.

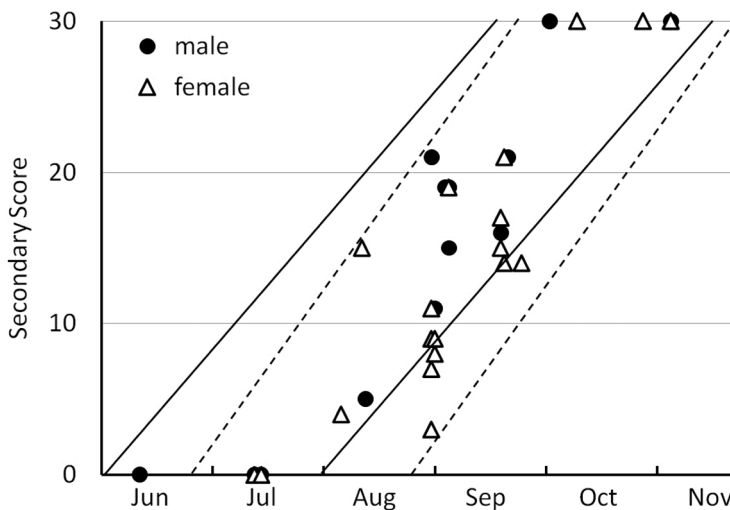


Figure 2. Scattergrams of secondary progression of Stripe-throated Bulbul show moult differences between the sexes. Regression of secondary moult scores against date of males and females, starting on 1 July, were $y = 0.263x - 1.649, R^2 = 0.824$ ($n = 11$), and $y = 0.297x - 8.666, R^2 = 0.626$ ($n = 16$), respectively. The lines, solid lines (males) and dash lines (females), indicate 95% confidence limits of each sex.

The estimated duration of primaries moult was ~136 days (males), and ~118 days (females). Moult of secondaries took ~114 days (males), and ~101 days (females). This compared with 112 days of primaries moult of the Yellow-vented Bulbul [8], 110 days of primaries moult of the Red-vented Bulbul (*P. cafer*) [31], and 126 days of primaries moult of the Grey-eyed Bulbul [9]. Duration of moult could be shaped by environmental constraints [14]. Moult following the breeding season of passerines is the most common moult strategy in migratory and non-migratory birds in order to have fresh flight feathers before the lean season [32]. Moult takes place over the rainy season when the forest has plenty of leaves, flowers, and fruits and a higher abundance of insects [8; 33]. This benefits feather synthesis since food abundance is most important for producing high quality feathers [5; 14]. Our data shows completion of moult of both sexes by mid November. The females start to moult later than the males but complete their moult at the same time. This result suggests that the dry season in this tropical forest is a lean period with lower food resources, lower temperatures, and reduced day-length.

Comparisons of wing moult by sex showed that males began moult earlier and took longer to complete the moult of both primaries and secondaries than the females. This result is consistent with previous studies that suggest that males generally moult earlier than females in some passerines. For example: males moult 14 days earlier than females in Yellow Canaries (*Crithagra flaviventris*) [34], 21 days earlier in Chestnut Weavers (*Ploceus rubiginosus*) [35], and 32 days earlier in Orange-breasted Sunbirds (*Anthobaphes violacea*) [34]. This result supports the idea that moulting is an

energetically expensive process [4, 6, 36, 37] and emphasizes that variation in energy expenditure during the breeding season can affect moult differentiation between the sexes. In general, males tend to invest earlier in reproduction by singing, establishing territories, defending territories and pursuing females, while females expend their reproductive energy on egg production, and may be more responsible for egg incubation and nestling care. In other bulbuls females spend more time in incubation and nestling care. Female Puff-throated Bulbuls (*Alophoixus pallidus*) build the nest and incubates eggs [38].

Our study had added to the understanding of the moult in the Stripe-throated Bulbul which, along with most other small birds in Thailand, had a complete post-nuptial moult during the rainy season. Our analyses suggested that there were significant moult differences between the sexes, males started moult earlier than females and had longer moult duration than females. We used the simple regression method for estimating moult duration because of the small sample sizes. This method, however, gave a slightly long duration of moult [9; 30]. Greatly increased sample sizes and multiple years of data collection are required to predict how moult might be impacted by environmental factors particularly climate change. Understanding the adaptive significance of this sexual difference in moult timing and duration requires more detailed investigation. Useful further investigations may be addressed by examining food availability e.g. fruiting phenology and insect abundance and its importance for feather synthesis and quality. In addition, more exploration of parental activity of this species is needed to explain of why moult differs between the sexes.

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REFERENCES

- [1] Humphrey P.S. and Parkes K.C., An approach to the study of molts and plumages, *Auk*, 1959; **76**(1): 1-31. DOI 10.2307/4081839.
- [2] Serra L., Duration of primary moult affects primary quality in Grey Plovers *Pluvialis squatarola*, *J. Avian Biol.*, 2001; **32**(4): 377-380. DOI 10.1111/j.0908-8857.2001.320415.x.
- [3] Ginn H.B. and Melville G.R., *Moult in Birds*, BTO Guide 19, BTO, Tring, 1983.
- [4] Dolnik V.R. and Gavrilov V.M., Bioenergetics of molt in the Chaffinch (*Fringilla coelebs*), *Auk*, 1979; **96**(2): 253-264.
- [5] Murphy M.E. and King J.R., Energy and nutrient use during moult by white-crowned sparrows *Zonotrichia leucophrys gambelii*, *Ornis Scandinavica*, 1992; **23**(3): 304-313. DOI 10.2307/3676654
- [6] Klaassen M., Moulting and basal metabolic costs in males of two subspecies of stonechats: The European *Saxicola torquata rubicula* and the East African *S. t. axillaris*, *Oecologia*, 1995; **104**: 424-432. DOI 10.1007/BF00341339.
- [7] Bridge E.S., Influences of morphology and behavior on wing-molt strategies in seabirds, *Marine Ornithol.*, 2006; **34**: 7-19.
- [8] Ward P., The annual cycle of the yellow-vented bulbul *Pycnonotus goiavier* in a humid equatorial environment, *J. Zoological Soc. London*, 1969; **157**: 25-45. DOI 10.1111/j.1469-7998.1969.tb01687.x.
- [9] Pierce A.J., Observations on breeding and moulting of the grey-eyed bulbul, *Iole propinqua*, in Thailand, *The Raffles Bull. Zool.*, 2009; **57**(1): 207-211.
- [10] Salewski V., Altwegg R., Erni B., Falk K.H., Bairlein F. and Leisler B., Moulting of three Palaearctic migrants in their west African wintering quarters, *J. Ornithol.*, 2004; **145**: 109-116. DOI 10.1007/s10336-004-0020-2.
- [11] Wilson J.D., Akriotis T., Balmer D.E., Hatton L. and Millar S., Biometrics and wing moult of migrating red-rumped swallows *Hirundo daurica* in Greece, *Ringed & Migration*, 2006; **23**: 57-61. DOI 10.1080/03078698.2006.9674345.
- [12] Round P.D., Gale G.A. and Nimnuan S., Moulting of primaries in long-toed stints (*Calidris subminuta*) at a non-breeding area in Thailand, *Ringed & Migration*, 2012; **27**(1): 32-37. DOI 10.1080/03078698.2012.691344.

- [13] McGregor R.M., Ottosson U. and Cresswell W.R.L., Moults of Guinea savanna passerines in west Africa, *Ostrich*, 2007; **78(2)**: 287-290. DOI 10.2989/OSTRICH.2007.78.2.26.106.
- [14] Barta Z., McNamara J.M., Houston A.I., Weber T.P., Hedenström A. and Feró O., Optimal moult strategies in migratory birds, *Philos. T. R. Soc. B. Biol. Sci.*, 2008; **363**: 211-229. DOI 10.1098/rstb.2007.2136.
- [15] Bell B.D., Moults in the Reed Bunting - A preliminary analysis, *Bird Study*, 1970; **17(3)**: 269-281. DOI: 10.1080/00063657009476284.
- [16] Khamcha D., Savini T., Brockleman W.Y., Chimchome V. and Gale G.A., Influence of food availability and distribution on the movement patterns of a forest avian frugivore, the Puff-throated bulbul (*Alophoixus pallidus*), *J. Trop. Ecol.*, 2012; **28**: 1-9. DOI: <http://dx.doi.org/10.1017/S026646741100054X>.
- [17] Lekagul B. and Round P.D., *A Guide to The Birds of Thailand*. Sahakarnbhaet, Bangkok, Thailand, 1991.
- [18] Robson C., *A Field Guide to The Birds of Thailand and South-east Asia*, Asia Books Company, Bangkok, Thailand, 2000.
- [19] Kitamura S., Yumoto T., Poonswad P., Chuailua P., Plongmai K., Maruhashi T. and Noma N., Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand, *Oecologia*, 2002; **133**: 559-572. DOI 10.1007/s00442-002-1073-7.
- [20] Singkaraj N., *A Survey of Seed-dispersing Birds of Macaranga Denticulata (Bl.) M.-A. at Doi Chiang Dao Wildlife Research Station, Chiang Dao District, Chiang Mai Province*, MS Thesis, Chiang Mai University, Thailand, 2010.
- [21] Maxwell J.F., Lowland vegetation (450-800 m) of Doi Chiang Dao Wildlife Sanctuary, Chiang Mai Province, Thailand, *Tigerpaper FAO*, 1992; **19(3)**: 21-25.
- [22] Maxwell J.F., Vegetation of Doi Tung, Chiang Rai province, northern Thailand, *Maejo Int. J. Sci. Technol.*, 2007; **1(01)**: 10-63.
- [23] Vaidhayakarn C. and Maxwell J.F., Ecological status of the lowland deciduous forest in Chang Kian valley, Chiang Mai, northern Thailand, *Maejo Int. J. Sci. Technol.*, 2010; **4(02)**: 268-317.
- [24] Round P.D., Gale G.A. and Brockelman W.Y., A comparison of bird communities in mixed fruit orchards and natural forest at Khao Luang, southern Thailand, *Biodivers. Conserv.*, 2006; **15**: 2873-2891. DOI 10.1007/s10531-005-2006-7.
- [25] Nakwa A., Sitasuwan N., Jatisatein A., Chantaramongkol P., Pupichit W. and Srisakb P., Bird diversity relative to forest types and physical factors at Tung Salang Luang National Park, Thailand, *Res. J. Biol. Sci.*, 2008; **3(6)**: 601-608.
- [26] Griffiths R. and Korn R.M., A CHD1 gene is Z chromosome linked in the chicken *Gallus domesticus*, *Gene*, 1997; **197**: 225-229. DOI 10.1016/S0378-1119(97)00266-7.
- [27] Sankamethawee W., Hardesty B.D. and Gale G.A., Sex-bias and timing of natal dispersal in cooperatively breeding puff-throated bulbuls *Alophoixus pallidus*, *J. Ornithol.*, 2010; **151**: 779-789. DOI 10.1007/s10336-010-0511-2.
- [28] Kocher T.D., Thomas W.K., Meyer A., Edwards S.V., Pääbo S., Villablanca F.X. and Wilson A.C., Dynamics of mitochondrial DNA evolution in

- animals: Amplification and sequencing with conserved primers, *Proc. Nat. Acad. Sci. USA*, 1989; **86**: 6196-6200.
- [29] Wu C.P., Horng Y.M., Wang R.T., Yang K.T. and Huang M.C., A novel sex-specific DNA marker in Columbidae birds, *Theriogenology*, 2007; **67**: 328-333. DOI 10.1016/j.theriogenology.2006.08.001.
- [30] Underhill L.G. and Zucchini W., A model for avian primary moult, *Ibis*, 1988; **130**: 358-372. DOI 10.1111/j.1474-919X.1988.tb08810.x.
- [31] Dhondt A.A., Breeding and postnuptial molt of the red-vented bulbul in western Samoa, *Condor*, 1977; **79(2)**: 257-260. DOI 10.2307/1367170.
- [32] Svensson E. and Hedenström A., A phylogenetic analysis of the evolution of moult strategies in western Palearctic warblers (Aves: Sylviidae), *Biol. J. Linn. Soc.*, 1999; **67**: 263-276. DOI 10.1006/bijl.1998.0302.
- [33] Swaddle J.P. and Witter M.S., Food availability and primary feather molt in European starlings, *Sturnus vulgaris*, *Can. J. Zool.*, 1997; **75**: 948-953. DOI 10.1139/z97-114.
- [34] Bonnevie B.T. and Oschadleus H.D., Timing of primary wing moult in sexually dimorphic passerines from the western Cape, south Africa, *Ostrich*, 2010; **81(1)**: 63-67. DOI 10.2989/00306525.2010.455821.
- [35] Oschadleus H.D. and Osborne T., Chestnut weaver *Ploceus rubiginosus* biometrics and primary moult in Namibia, *Ostrich*, 2005; **76**: 206-211. DOI 10.2989/00306520509485494.
- [36] Dietz M.W., Daan S. and Masman D., Energy requirements for molt in the Kestrel *Falco tinnunculus*, *Physiol. Zool.*, 1992; **65(6)**: 1217-1235. DOI 10.2307/30158276.
- [37] Lindström A., Visser G.H. and Daan S., The energetic cost of feather synthesis is proportional to basal metabolic rate, *Physiol. Zool.*, 1993; **66(4)**: 490-510.
- [38] Pierce A.J., Tokue K., Pobprasert K. and Sankamethawee W., Cooperative breeding in the puff-throated bulbul *Alophoixus pallidus* in Thailand, *The Raffles Bull. Zool.*, 2007; **55(1)**: 187-189. DOI 10.1016/j.bse.2014.03.032.