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Physical Traits of Male Japanese Bush Warblers (*Cettia diphone*) in Summer and Winter: Hyperactive Aspects of the Vocal System and Leg Muscles in Summer Males

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The Japanese bush warbler has a very distinctive song, shows marked sexual size dimorphism, and has a polygynous mating system. However, the physical traits of males and seasonal variation in such traits have remained unknown. Twenty-five anatomical measurements representing physical traits of males in the breeding (summer, n = 5) and non-breeding (winter, n = 5) seasons were examined morphologically and compared statistically. Differences were evident between summer and winter ($P < 0.05$, t test) in the following seven items: body mass (19.8 ± 0.7 g *vs.* 15.6 ± 1.2 g [mean ± SD]), mass of male reproductive organs (184.0 ± 25.7 mg vs. 6.0 ± 1.4 mg), hind limb (3789.2 ± 346.2 mg vs. 3003.4 ± 226.8 mg), leg muscles (883.0 ± 63.5 mg vs. 581.4 ± 33.2 mg in either side), skin around the neck/throat (1280 ± 34.9 mg vs. 287.2 ± 84.7 mg), and syrinx (35.8 ± 2.39 mg vs. 25.0 ± 3.24 mg), and circumference of the neck/throat (52.1 ± 2.3 mm vs. 38.3 ± 2.6 mm). In contrast to winter males, summer males had thickened flabby skin prominently in the neck/throat area and an inflatable esophagus, perhaps a morphological basis for the throat sac as a vocal resonator. Also, the remarkable development of the flexor muscles of the legs of summer males suggests that perching and movement using the legs increases during the breeding season. These distinct characteristics of summer males may be related to the polygynous mating system of this species.

Key words: Japanese bush warbler, male, physical traits, polygyny, sexual size-dimorphism

INTRODUCTION

The Japanese bush warbler (*Cettia diphone*) is one of the best-known passerines in Japan and occurs along the eastern rim of the Eurasian continent and the Japanese islands. This sedentary and migratory species inhabits dense shrubbery and thickets in open country or secondary forest. Externally, both sexes have drab, dull-colored plumage, but show a remarkable male-biased sexual size dimorphism (SSD). Males are larger than females by 18.8% in wing length and 70.4% in body mass (Hamao, 1992). During the breeding season, males are highly territorial and defend their territory with territorial songs, but do not participate in parental care (Haneda and Okabe, 1970; Hamao, 1992). Their songs are loud and very distinctive, with two variations described (Baker, 1997). The first, the common song, consists of an introductory whistle and an ending syllable. The second is referred to as the longer song (Baker, 1997) or long calls (Wada et al., 1999), and consist of a series of double notes. As to the common song, two subtypes have been discriminated and designated as H (H1 and H2 in details) and L (Hamao, 1993; Momose, 1999) or alpha and beta (Park and Park, 2000). It has been suggested that alpha songs are specialized for mate attraction and beta for territorial defense, although they function complementarily (Park and Park, 2000). Furthermore, it should be noted that the Japanese bush warbler (hereafter bush warbler) has a polygynous mating system (Haneda and Okabe, 1970; Hamao, 1992). Hamao (1992) strongly suggested that this mating system was an advanced form of polygyny characterized by a lack of a pair bond. Focusing on this mating system, Wada et al. (1999) studied behavioral and hormonal aspects of territorial bush warbler males and found that high levels of circulating testosterone and corticosterone continue during a prolonged period in the breeding season, unlike in “typical” monogamous species, in which hormone levels are generally high only during an early, short period of the breeding season. In male bush warblers, these differences in hormone levels during the breeding season may allow them to pursue a polygynous breeding strategy, to hold a territory, and to maintain breeding activity for a prolonged period, characteristics considered likely to be adaptations to dense habitat with high rates of predation and brood parasitism (Wada et al., 1999).

However, very little is known about the seasonal variation in physical traits in sexually dimorphic birds, including the bush warbler (Beck and Braun, 1978; Greenberg et al., 2013). According to Wada et al. (1999) in a study of male

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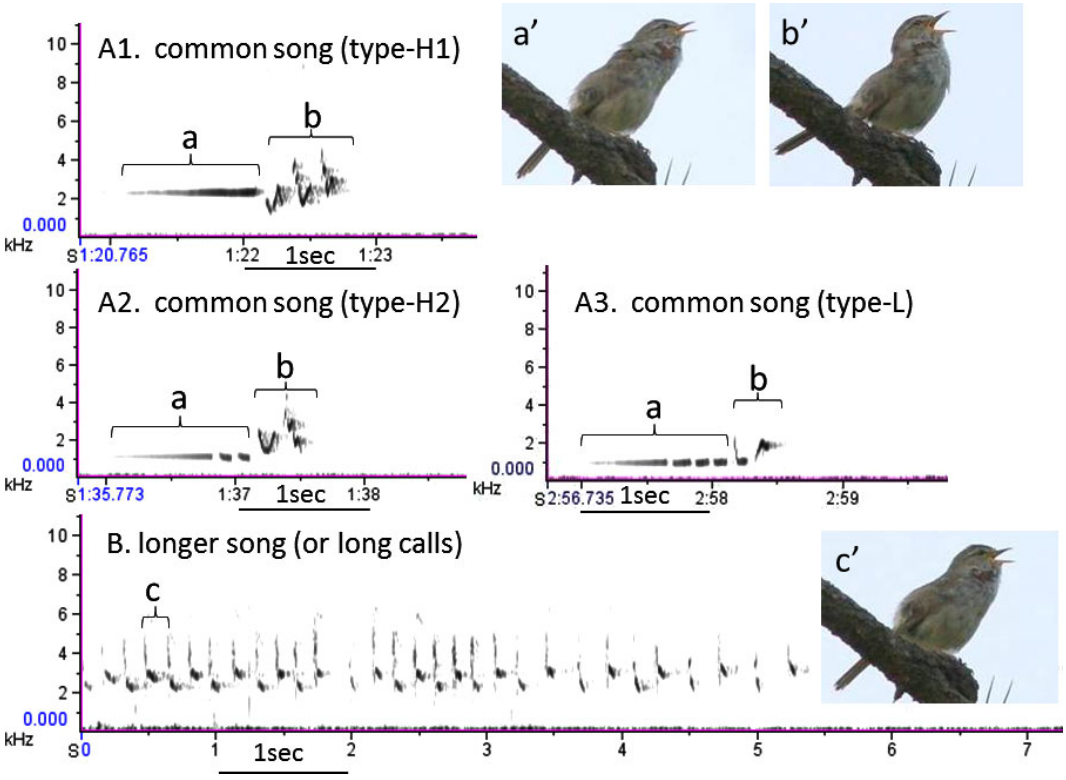


Fig. 1. Sonograms of the common song **(A1–3)** generally known as type-H1, H2, and L, and the longer song **(B)** of Japanese bush warbler showing their vocal components, i.e., leading whistle (a) and ending syllable (b) in the former and a series of double notes (c) in the latter. The postures (a′, b′, and c′) of singing males correspond with the vocal components, a, b, and c, in the type -H1 and the type-L, respectively.

bush warblers, high body mass values were maintained from May to July, but decreased significantly in August. This tendency was confirmed by our preliminary studies (unpublished data), but its biological significance has not been explained. Furthermore, during the breeding season, male bush warblers show other physical traits, e.g., increased neck/throat size and stronger toe grip (unpublished data). The anatomical basis and biological significance of these traits also remain to be established.

The aims of the study reported here were to address these subjects, based on both field and laboratory studies.

MATERIALS AND METHODS

Records of singing behaviors and songs

Field studies were carried out at a coastal pine forest in Niigata City (37°54′N, 139°02′E). Data, songs, and singing postures of territorial males, were recorded using a linear PCM recorder (LS-7, Olympus, Tokyo), a digital camera (7D, Canon, Tokyo) equipped with a 400 mm lens, and a handheld video camera (TVR240K, Sony, Tokyo). Acoustic data (31 files recorded from five males, about 68 min in total recording time) were converted to sonograms using Raven Lite Ver. 1.0 software (Bioacoustic Research Program, Cornell Laboratory of Ornithology) and studied in combination with singing behaviors. Details of sonograms were analyzed in comparison with the previous data on the present subspecies (Hamao, 1993; Momose, 1999).

Animals and treatments

We captured a total of 200 birds (97 males and 103 females) for banding study in the field throughout the period 2011–2012. All these birds belong to a subspecies, *C. d. cantans,* and are generally



Fig. 2. Photograph of a male bush warbler uttering the common song. Note his inflated throat, a sac-like structure, showing a patch of bare skin (white arrow).

regarded as resident breeder in Honshu (The Ornithological Society of Japan, 2012). All treatments complied with the *Guidelines for the Care and Use of Laboratory Animals in Nippon Dental University School of Life Dentistry at Niigata*. To minimize the number of birds sacrificed in this study, we carefully selected ten adult males as a sample. They were collected (with permission from the Ministry of the Environment of Japan, License number 110712002) during their breeding and non-breeding seasons (five in late May and five in late December, 2012) in riparian forests in Saitama Prefecture (36°02′N, 139°23′E, 35 m above sea level). For convenience, they will be referred to as summer or winter males, respectively. The birds were euthanized by anesthetizing them deeply with isoflurane (Interpet

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Table 1. Comparison of physical traits of male bush warbler, *Cettia diohone*, between breeding (summer) and non-breeding (winter) seasons.

Samples (number) Measurement items	Summer male (n = 5)	Winter male (n = 5)	Difference of numericals
Wing length (mm)	64.2 ± 0.9	64.1 ± 1.3	ns
Tail length (mm)	66.6 ± 1.2	66.6 ± 5.5	ns
Bill length (mm)	12.3 ± 1.1	12.9 ± 0.4	ns
Tarsus, length (mm)	25.3 ± 0.6	25.7 ± 0.7	ns
depth (mm)	2.1 ± 0.1	2.2 ± 0.1	ns
width (mm)	1.5 ± 0.0	1.4 ± 0.1	ns
Hallux, length (mm)	8.4 ± 0.3	8.5 ± 0.5	ns
width (mm)	2.0 ± 0.1	1.9 ± 0.2	ns
3rd toe, length (mm)	12.5 ± 0.8	13.5 ± 0.6	ns
width (mm)	1.5 ± 0.1	1.4 ± 0.1	ns
Body mass (g)	19.8 ± 0.7	15.6 ± 1.2	$P < 0.05$
Body volume (ml)*,#	21.0 ± 3.7	16.8 ± 1.3	ns
Mass of male reproductive organs (mg)*	184.0 ± 25.7	6.0 ± 1.4	$P < 0.05$
Liver mass (mg)*	839.0 ± 268.5	596.2 ± 85.9	ns
Heart mass (mg)*	452.0 ± 86.38	389.2 ± 44.7	ns
Mass of visceral and subcutaneous fat (mg)*	186.0 ± 56.4	317.6 ± 118.7	ns
Circumference of the neck/throat (mm)*	52.1 ± 2.3	38.3 ± 2.6	$P < 0.05$
Mass of skin around the neck/throat (mg)*	1,280.8 ± 34.9	287.2 ± 84.7	$P < 0.05$
Syrinx mass (mg)*	35.8 ± 2.39	25.0 ± 3.24	$P < 0.05$
Pectoral muscles mass, both sides (mg)*	2,420.2 ± 184.2	2,278.4 ± 161.8	ns
Forelimb mass, both sides (mg)*	835.8 ± 103.3	939.8 ± 77.5	ns
Hindlimb mass, both sides (mg)*	3,789.2 ± 346.2	3,003.4 ± 226.8	$P < 0.05$
Thigh muscles mass, either side (mg)*	541.2 ± 51.4	477.8 ± 25.5	ns
Leg muscles mass, either side (mg)*	883.0 ± 63.5	581.4 ± 33.2	$P < 0.05$
Mass of skeleton and bare parts, either side (mg)*	381.2 ± 26.2	383.4 ± 38.4	ns

*, measurements after fixation; ns, not significant.
#, measurements of the whole body without feathers.

Co. Ltd., Tokyo), they were then weighed and measured. The bodies were next soaked in a fixative containing 50% ethanol and 5% formaldehyde for several minutes and their feathers were removed. The featherless samples were post-fixed and kept in a fresh solution of 5% formalin, and used for anatomical examination.

X-ray computed tomography (CT) and image processing

Two fixed samples (one male per season) were rinsed in tap water and scanned using a micro-CT scanner (3DX Multi Image Micro CT FPD8: Morita, Kyoto) with X-ray source, 70.0 kV; 5.0 mA. Micro-CT images were then reconstructed using 3D structural analysis software (One Volume Viewer, Morita, Kyoto) and viewed using a personal computer.

Anatomical examination

The fixed samples were rinsed thoroughly in tap water and examined macroscopically. Excess water was absorbed with tissue paper, after which various organs and body portions were dissected out, measured with a Vernier caliper to the nearest 0.1 mm, or weighed on an electronic balance to the nearest 0.1 mg. Before dissection, the whole body volume was estimated as the water volume corresponding to the sample volume in the measuring cylinder. To keep standard of dissection, the syrinx was cut out at the level of 10th tracheal ring and 10th bronchial ring. The forelimbs and hind limbs were separated from the trunk at the

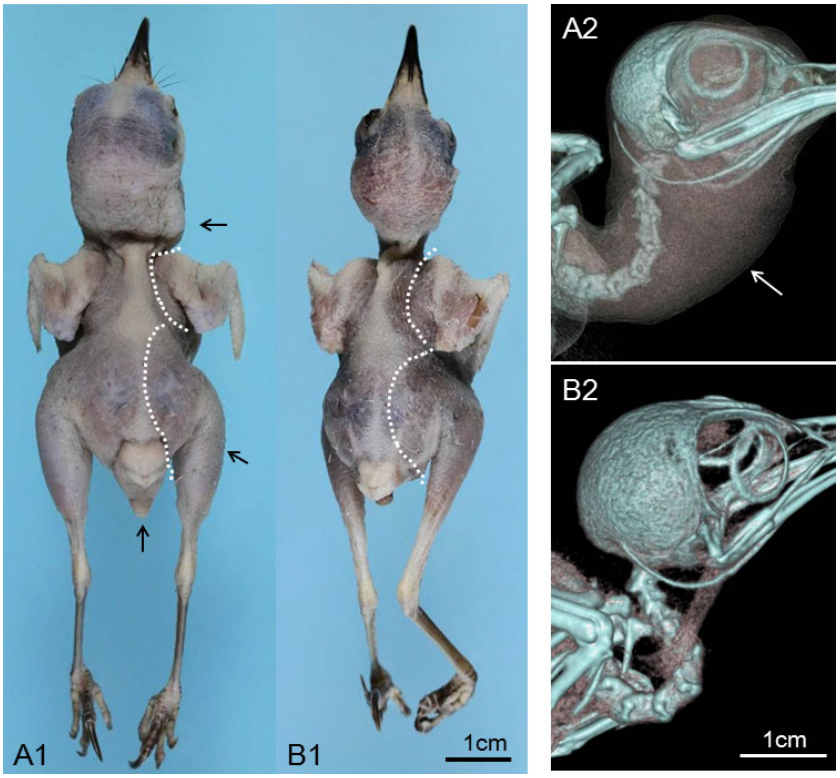


Fig. 3. Comparison of the physical condition of male Japanese bush warbler between summer **(A1, 2)** and winter **(B1, 2)**. A1 and A2, dorsal view of the featherless samples; A2 and B2, lateral view of X-ray CT-images of head portions. Note the hypertrophy of neck/throat, leg, and cloacal protuberance in the summer male (arrows in **(A1, 2)**). Broken lines in **(A1)** and **(B1)**, were shown as standard cutting line for dissection of forelimbs and hind limbs.

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level of their proximal end (broken lines in Fig. 3-A1, B1). The skin of neck/throat was cut out cranially at the level from posterior end of the cranium to chin (broken line x in Fig. 4-A1, B1) and caudally at the level of near the end of neck (broken line y in Fig. 4-A1, B1). Circumference of the neck/throat was measured at the level of middle of neck length (along the line a–b in Fig. 4-A1, B1). Anatomical organization of the skeletal muscles and tendons was studied with a stereoscopic microscope. The nomenclature used for designating the muscles of the hind limb in the present study were adopted from Verstappen et al. (1998) and that used for the syringeal muscles from Ames (1971).

Statistical analysis

Measurements (average ± SD) were statistically analyzed by student's *t* test and differences were considered significant when $P < 0.05$.

RESULTS

Songs and singing behaviors

Two song variants, the common song and the longer song, were readily identified in the sonograms, based on voice recordings made in the wild (Fig. 1) and subtypes of the common song (H1, H2, and L) which we obtained from different males showed a general sonogram pattern for these elements (Fig. 1).

Prior to commencing the common song, males began to inflate the throat sac with air, the beak was partly open and the head and body were in a high position; birds seemed to be silent during this phase. Then, simultaneously with maximum inflation of the throat sack being achieved, an introductory whistle was uttered (Fig. 1a′, 2) followed quickly by an ending syllable. At this moment, the beak was directed upward and fully opened and the chin quivered, but the bulging of the throat sack was rather inconspicuous probably due to minor deflation (Fig. 1b′). During the inflation of the throat, a small patch of bare skin resembling a drumhead became visible on either side of the throat (Fig. 2). The posture for the longer song resembled that for the introductory whistle of the common song, but the beak was open wider (Fig. 1c′). Thus, throat inflation was simultaneous

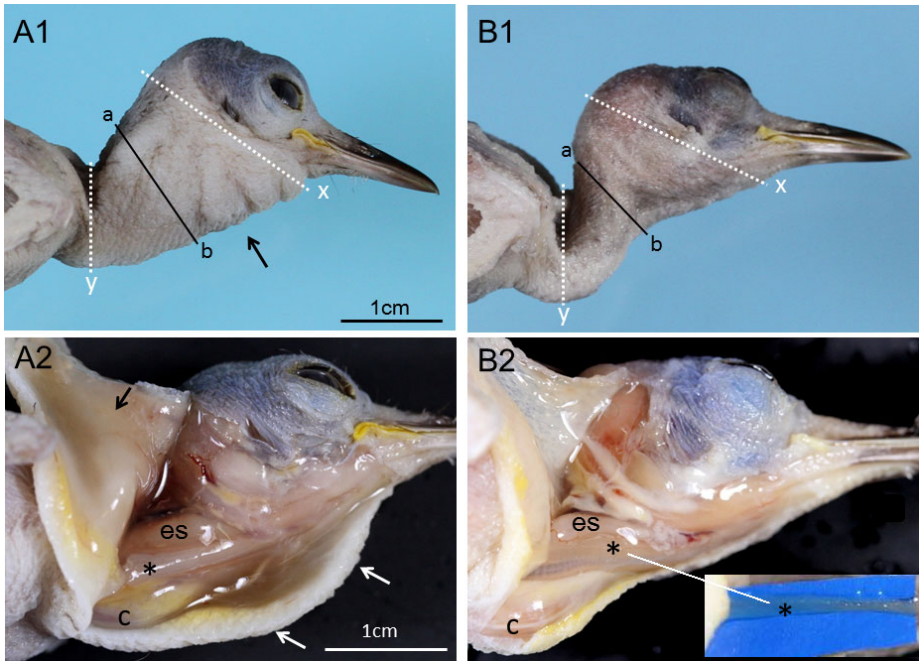


Fig. 4. Comparison of the neck/throat portion of male Japanese bush warbler between summer **(A1, 2)** and winter **(B1, 2)** to show remarkably hypertrophied throat in the summer male (arrows in **(A1, 2)**). **(A1)** and **(B1)**: lateral view; **(A2)** and **(B2)**, internal view after partial dissection. Note the thickened flabby skin (white arrows in **(A2)**) lined with thicker connective tissue (black arrow in **(A1)**). c, cervical muscle; es, esophagus; asterisk (*), sternohyoid muscle (*m. sternohyoideus*). The skin of neck/throat between broken lines x and y was dissected out for measurement and the circumference of the neck/throat was measured along the line a-b in **(A1)** and **(B1)**.

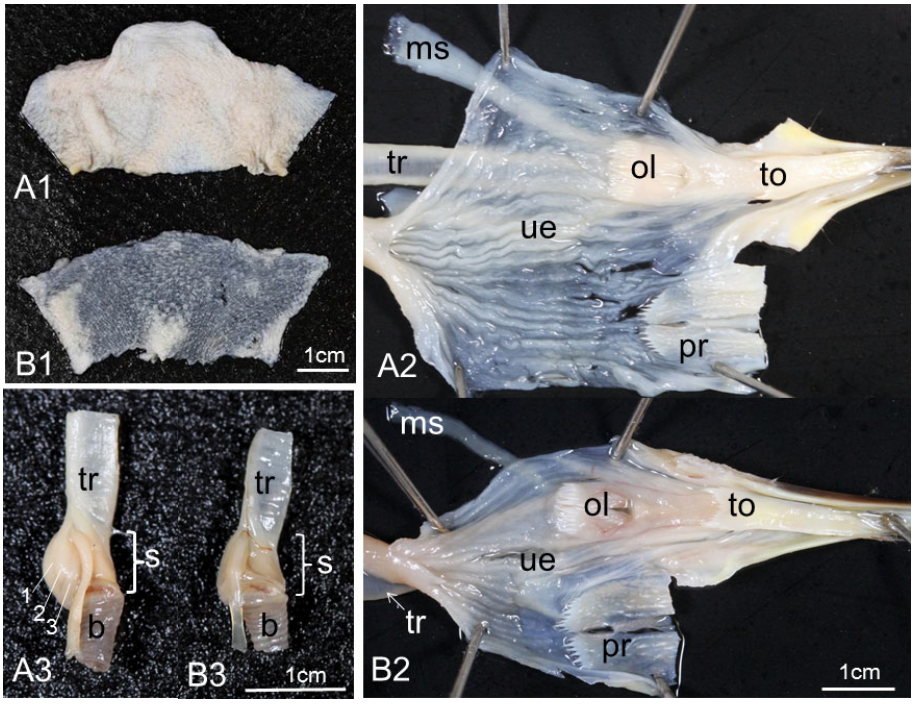


Fig. 5. Comparison of the skin around the neck/throat (**(A1)** and **(B1)**, ventral view), the upper esophagus (**(A2)** and **(B2)**, dorsal view, anterior to the right), and the syrinx (**(A3)** and **(B3)**, lateral view, cranial to the top) between summer (**A1–3**) and winter **(B1–3)**. b, left bronchus; ms, *musculus strenohyoideus*; ol, laryngeal opening; pr, pharyngeal roof; s, syrinx; tr, trachea; to, tongue, ue, upper esophagus; 1–3, syringeal muscles, *musculus bronchialis anticus*, *m. bronchotrachealis anticus*, and *m. sternotrachealis*, respectively.

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with the utterance of territorial songs, with deflation occurring after songs were completed. This pattern of singing behavior was most distinct in H type song.

Measurements

For evaluation of the physical traits of summer and winter males, 25 anatomical features were examined macroscopically and their dimensions and masses were compared statistically (Table 1). Clear differences were found between summer and winter ($P < 0.05$ by t test) in the following seven features: body mass (19.8 ± 0.7 g vs. 15.6 ± 1.2 g [mean ± SD]), mass of male reproductive organs (184.0 ± 25.7 mg vs. 6.0 ± 1.4 mg), skin around the neck/throat (1280 ± 34.9 mg vs. 287.2 ± 84.7 mg), syrinx (35.8 ± 2.39 mg vs. 25.0 ± 3.24 mg), hind limbs (3789.2 ± 346.2 mg vs. 3003.4 ± 226.8 mg), leg muscles (883.0 ± 63.5 mg vs. 581.4 ± 33.2 mg on either side), and circumference of the neck/throat (52.1 ± 2.3 mm vs. 38.3 ± 2.6 mm). However, no significant differences were found in other features (Table 1).

Gross morphology and anatomical features

On external view, summer male samples showed remarkable development around the neck/throat, hypertrophy of the hind limbs, and cloacal protuberance (Fig. 3-A1–B1). X-ray CT confirmed dramatic seasonal differences in the neck/throat (Fig. 3-A2–B2). Dissection revealed that, in contrast to winter males, summer males had thickened flabby skin and well-developed dermal connective tissue in the neck/throat area (Figs. 3-A1–B1, 4-A1–B1, 5-A1–B1), more flexible and dilated condition of the upper esophagus (Fig. 5-A2–B2), and thicker sternohyoid muscle *m. sternohyoideus* (Fig. 4-A2–B2, Fig. 5-A2–B2). Similarly, the syrinx of summer males was very massive due to hypertrophy of the syringeal muscles, mainly *musculus bronchialis anticus*, *m. bronchotrachealis anticus*, and *m. sternotrachealis* (Fig. 5-A3–B3). These differences were evaluated by the mass of the syrinx with associated portions of the trachea and bronchus (Table 1). The difference in the mass of the hind limbs between summer and winter was statistically significant (Table 1) and ascribed exclusively to the physical condition of the leg muscles, not to that of other components of the hind limbs, i.e., thigh muscles and skeleton/bare parts (Tables 1, 2; Fig. 6). Of all the leg muscles identified, three flexor muscles (MFDL *m. f. digitorum longus*, MFHL *m. f. hallucis longus*, and MFPD3 *m. f. perforatus d3*) weighed from 1.9 to 3.7 times more in summer than in winter (Table 2). In the anisodactylic arrangement of the toes, these muscles were anatomically disposed to generate grip force by pulling their tendons; a robust tendon of MFHL was sent

Table 2. Comparison of leg muscles mass of male bush warbler between summer and winter.

Samples (number) measurement items (mg)*, #	Summer male (n = 5)	Winter male (n = 5)	Difference of numericals
MEDL	22.2 ± 2.9	20.4 ± 1.8	ns
MFB	28.8 ± 11.0	16.4 ± 1.1	ns
MFDL	88.8 ± 6.6	46.2 ± 5.5	$P < 0.05$
MFHL	237.2 ± 25.5	92.2 ± 5.7	$P < 0.05$
MFL	124.6 ± 13.8	92.8 ± 13.8	ns
MFPD2	17.0 ± 1.9	13.4 ± 1.1	ns
MFPD3	30.8 ± 7.8	8.4 ± 9.4	$P < 0.05$
MFPD4	33.2 ± 7.5	32.4 ± 3.6	ns
MFPPD2	5.8 ± 0.4	4.2 ± 1.3	ns
MFPPD3	22.4 ± 7.9	27.6 ± 2.4	ns
MG (MGI+MGL+MGM)	220.2 ± 9.9	186.6 ± 17.1	ns
MTC	52.0 ± 6.7	40.8 ± 2.8	ns

*, Abbreviations: Non-abbreviated nomenclatures were shown in the legend of Fig. 6.
#, Measurements on either side of the legs after fixation.
ns, not significant.

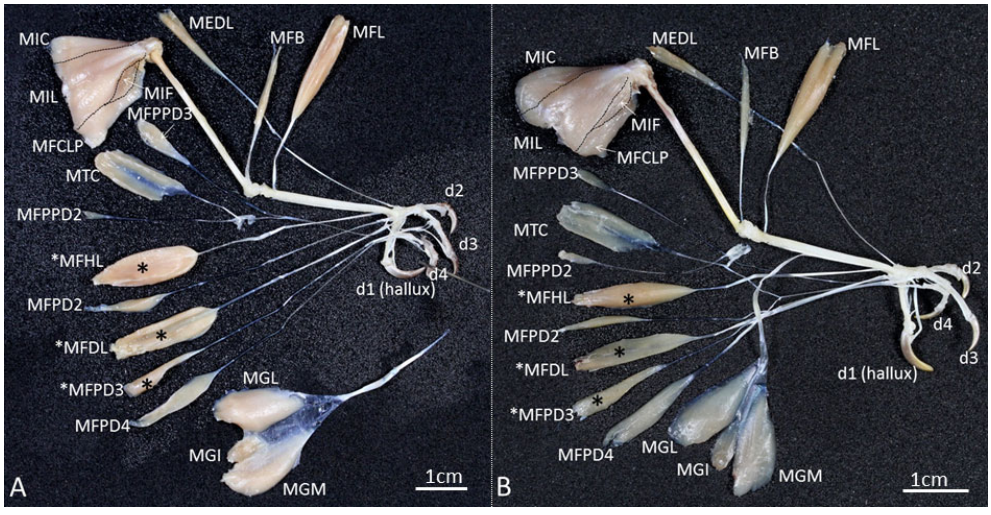


Fig. 6. Comparison of the skeletal muscles of the hind limb (right side) between summer **(A)** and winter **(B)**. Leg muscles were dissected out and re-arranged to show different physical conditions of several components (*). d1, hallux; d2–d4, digitus 2–4. Nomenclatures for abbreviations: MEDL *musculus extensor digitorum longus*, MFB *m. fibularis brevis*, MFCLP *m. flexor cruris lateralis pars pelvica*, MFDL *m. flexor digitorum longus*, MFHL *m. flexor hallucis longus*, MFL *m. fibularis longus*, MFPD2 *m. flexor perforatus d2*, MFPD3 *m. flexor perforatus d3*, MFPD4 *m. flexor perforatus d4*, MFPPD2 *m. flexor perforans et perforatus d2*, MFPPD3 *m. flexor perforans et perforatus d3*, MGI m. *gastrocnemius pars intermedia*, MGL m. *gastrocnemius pars lateralis*, MGM m. *gastrocnemius pars medialis*, MIC m. *iliotibialis cranialis*, MIF m. *iliofibularis*, MIL m. *iliotibialis lateralis*, MTC m. *tibialis cranialis*.

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distally to the hallux (hind toe), while others derived from MFPD3 and MFDL reached oppositely to the second, third, and fourth toes (front toes). The male reproductive organs (the testis, epididymis, and ductus deferens) were massive and remarkably developed in summer males in strong contrast to those in winter males. These morphological changes were clearly reflected in the mass of these organs (Table 1).

DISCUSSION

Biological significance of body mass variations

Major findings of the present study on the bush warbler concern the development of three different organs or systems in summer males, i.e., (1) the male reproductive organs, (2) the vocal system represented by the syrinx and inflatable throat, and (3) the hind limbs as a locomotion system. Characteristics of these organs or systems explain the greater body mass of summer males described for this species (Wada et al., 1999). Increased body mass in male bush warblers is a consequence of seasonal magnification of the secondary sexual characteristics, but does not result from changes in other physical items, e.g., stored fat. It has long been known that, in passerines, subcutaneous energy reserves (fat deposition) increase in winter and decline in summer (Lehikoinen, 1987; Haftorn, 1989), for fat constitutes the major source of metabolic fuel during winter fasts such as sudden harsh conditions and long cold nights (Blem, 1990; Krams et al., 2010). This is not the case in male bush warblers. Thus, we suggest that seasonal variations in body mass may reflect species-specific biological backgrounds and other as-yet undescribed factors.

Vocal system

Morphological aspects of the syrinx, upper esophagus and skin around the neck/throat of summer males seem to be functionally and anatomically related with each other and serve to elaborate the developed vocal system in the breeding season. The syrinx is the primary vocal (sound-producing) organ unique in birds and its anatomical structure and mechanisms of vocalization have been well documented (Ames, 1971; King, 1989; Evans and Heiser, 2004). Zebra finch *Taenipygia guttata* (Riede and Goller, 2010) and common starling *Sturnus vulgaris* (Prince et al., 2011) each have a sexually dimorphic syrinx, reflecting sexual differences in vocal behavior. In zebra finch, the syrinx of males is about twice as heavy as that in females and a much larger muscle mass and the more robust syringeal skeleton in males enable generation of their greater fundamental frequency range during vocalization. In the bush warbler, the much larger syringeal muscles in summer males are reasonably correlated with seasonal differences in vocal behaviors; males utter calls and songs during the prolonged breeding period in summer (Wada et al., 1999), but only calls in winter.

Qualitative changes of the upper esophagus in summer males support the view that the esophagus is primarily responsible for inflation of the throat in combination with the flabby skin. In fact, the throat is inflated simultaneously with the utterance of territory songs, thus it is reasonable to consider that the upper esophagus and the associated skin lined with well-developed dermal connective tissue serve together to elaborate the throat sac as a vocal resonator, as seen in non-oscine birds (Chapin, 1922; Riede et al., 2004). This may allow the vocal signals generated in the syrinx to be modified or amplified (into louder voice) so as to carry further (more efficient transmission) in the territory. In the bush warbler, which is adapted to habitat with dense shrubbery and thickets, this adaptation seems to be significant, allowing males to pursue territory defense and mate attraction by acoustic communication in dense habitat (Hamao, 1992; Wada et al., 1999; Park and Park, 2000). It is interesting that some non-oscine birds utilize the esophagus, which serves as a vocal resonator, for filtering and modifying the sounds generated by the syrinx, e.g., the emu *Dromaius novaehollandiae*, various grouse, pigeons and the American bittern *Botaurus lentiginosus* (Chapin, 1922; Evans and Heiser, 2004; Riede et al., 2004). Additionally, in some species, sacs (specialized out-pockets of the upper esophagus) protrude dramatically revealing bright-colored skin in male prairie-chickens and serve as visual signals that enhance the total display (Evans and Heiser, 2004). In the bush warbler, however, it remains unknown whether or not the inflated throat also provides a visual signal.

The sternohyoid muscle in the throat was found to be more developed in summer than in winter. Its function is enigmatic, but the anatomical arrangement of this muscle suggests a certain participation in controlling the movement of the throat skin, because it runs cranio-caudally under the skin and has partial abutments on the lining of the throat skin.

Biological significance of the developed hind limbs

Anatomical examination of the hind limbs of male bush warbler manifested three facts: (1) their mass was greater in summer than in winter, (2) this difference was ascribed to hypertrophy of the leg muscles, not to other structural components of the hind limb and (3) the muscular hypertrophy occurred in three flexors (MFHL, MFPD3 and MFDL), which were organized to generate grip force in the anisodactylic arrangement of the toes. These observations may explain the stronger toe grip of summer males and suggest a physical adaptation for locomotion, such as perching and movement using the legs, although little is known about the anatomical basis of perching locomotion (Zeffer et al., 2003; Abourachid and Höfling, 2012). This aspect suggests a possible relation of the physically developed hind limbs to certain changes of behavior or activities in males during the breeding season. However, the present study has no clear explanation for this subject. We speculate that this physical change may relate to the behavioral traits of summer males, i.e., defending their territories by active locomotion and territorial vocalization in dense habitat. According to Hamao (1992), territories of bush warbler are frequently intruded upon by non-residential males. In a polygynous mating system, such physical changes in the hind limbs may be advantageous to males concerning not only (1) locomotion for defending territory in such habitat, but also (2) mechanical support for balancing the body on song posts given the seasonally developed heavy neck/throat. Another possibility concerns a possible relation to increased activity of foraging in the shrubby territory, which may be supported by the fact that body mass increased during the breeding season. Such physical changes may be under hormonal influence (Balthazard, 1983;

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Wingfield, 1984; Wada et al., 1999), although experimental treatment by testosterone apparently has no significant effects on muscle mass gains in some birds (Alonso-Alvaretz et al., 2002; Buttemer et al., 2008). In the future, these points should be further investigated in addition to a possible relation to the mating system.

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