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Authors: Toki, Wataru, and Togashi, Katsumi

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Exaggerated Asymmetric Head Morphology of Female *Doubledaya bucculenta* (Coleoptera: Erotylidae: Languriinae) and Ovipositional Preference for Bamboo Internodes

Wataru Toki* and Katsumi Togashi

Laboratory of Forest Zoology, Department of Forest Science, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Yayoi 1-1-1, Bunkyo-ku, Tokyo 113-8657, Japan

The lizard beetle *Doubledaya bucculenta* (Coleoptera: Erotylidae: Languriinae) female has evident asymmetric head morphology. The females excavate small holes in host bamboo internodes for the deposition of eggs. To understand the asymmetry and allometry of male and female adults and larvae of *D. bucculenta*, mandibular length, genal and head width, and elytral length were measured, and the oviposition preference for different-sized internodes of the bamboo *Pleioblastus simonii* and the relationship between internode size and emerging adult size were examined. Larval mandibles exhibited no clear asymmetry pattern, and genae showed fluctuating asymmetry in length. Adult male mandibles showed left-directional asymmetry, but genae showed fluctuating asymmetry. Adult female mandibles and genae exhibited marked left-directional asymmetry. The degree of asymmetry of mandibles and genae remained constant regardless of body size. Large females tended to choose large-diameter internodes of *P. simonii* and to lay eggs successfully, whereas small females tended to choose intermediate-diameter internodes, but to fail in oviposition, suggesting that small females pay a high cost on oviposition. There was a positive correlation between internode size and emerging adult size. Marked directional asymmetry of female mandibles and genae are discussed in relation to greater frequency of cutting bamboo fibers compared with adult males, and the traits of bamboo internode.

Key words: lizard beetle, directional asymmetry, fluctuating asymmetry, mandible, gena, *Pleioblastus simonii*, allometry

INTRODUCTION

In animal species that exhibit bilateral asymmetry, the bilateral asymmetry of individual animals may play key roles in survival and/or reproduction. For example, scale-eating cichlid fish, snail-eating water-scavenger larvae, and snail-eating snakes increase foraging efficiency by asymmetric mouthparts (Hori, 1993; Inoda et al., 2003; Hoso et al., 2007). Male beetles of the genus *Agathidium* show superiority in male-to-male competition by asymmetric horns on mandibles (Miller and Wheeler, 2005). Hermaphroditic land snails with high-spired shells more frequently have two forms with reversally coiling shells, sinistrals and dextrals, than those with low-spired shells. The coexistence of the two forms is elucidated by greater interchiral mating success that is caused by shell-mounting mating behavior in snails with high-spired shells (Asami et al., 1998).

In a given population, there may be three types of bilateral asymmetry: fluctuating asymmetry (FA), indicating random deviations from symmetry; directional asymmetry (DA), indicating a lack or rarity of one of two possible mirror-image forms; and antisymmetry (AS), indicating equally common mirror-image forms (Van Valen, 1962; Palmer, 2005). DA of head morphology, especially mandibular traits, has recently been reported in beetles (Table 1). This type of asymmetry of mandibles may be connected with functions, such as feeding, boring, and/or fighting, in which mandibles often play important roles. However, only a few studies have shown the function and/or the significance of direction of asymmetry of the traits (Inoda et al., 2003; Miller and Wheeler, 2005; Table 1). Okada et al. (2008) suggested that DA in mandible of larval *Prosopocoilus inclinatus* Motschulsky (Lucanidae) may be related to cutting wood fibers in feeding.

Adult females of *Doubledaya bucculenta* Lewis also have larger left mandibles and genae than the right, a distinctive DA, whereas the male beetles have similar-sized left and right mandibles and genae (Lewis, 1884; Kurosawa et al., 1985). In spring, *D. bucculenta* adults make exit holes to emerge from dead internodes of bamboo culms of *Pleioblastus* sp., *P. simonii* Nakai, *P. chino* Makino and *Semiarundinaria* sp. (Hayashi, 1974; Toki, 2009). They eat foods on the surface of bamboo culms using maxillae. The females excavate small holes in internodes of newly dead

* Corresponding author. Phone: +81-3-5841-5207;
Fax : +81-3-5841-7555;
E-mail: watarutoki@08.alumni.u-tokyo.ac.jp
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Table 1. List of directional asymmetry of head morphology in beetles. [a]1, Oberprieler and Arndt, 2000; 2, Inoda et al., 2003; 3, Miller and Wheeler, 2005; 4, Hanley, 2001; 5, Okada et al., 2008; 6, Schunger et al., 2003; 7, Villiers, 1945; Wegrzynowicz, 2002; 8, Arrow, 1940; Sforzi and Bartolozzi, 2004.

Family	Genus/species	Developmental stage	Sex	Trait	Larger side	Behavior related to the asymmetry	Reference[a]
Carabidae	*Manticora* spp.	Adult	Male	Mandible	Right	Unknown	1
Hydrophilidae	*Hydrophilus acuminatus*	Larva	–	Mandible	Right	Predation of right-handed snails	2
Leiodidae	*Agathidium* spp.	Adult	Male	Mandible	Left	Male-to-male combat	3
Staphylinidae	*Oxyporus* (*Pseudoxyporus*) spp.	Adult	Male	Mandible	Right	Unknown	4
Lucanidae	*Prosopocoilus inclinatus*	Adult	Small male	Mandible	Left	Unknown	5
		Larva	–	Mandible	Left	Unknown	5
Prostomidae	*Prostomis mandibularis*	Larva	–	Gena	Left	Unknown	6
Erotylidae	*Doubledaya* spp.	Adult	Female	Mandible and gena	Left	Unknown	7
Brentidae	*Bolbocranius csikii*	Adult	Male	Mandible	Left	Unknown	8
	Bolbocranius distortus	Adult	Male	Mandible	Left	Unknown	8

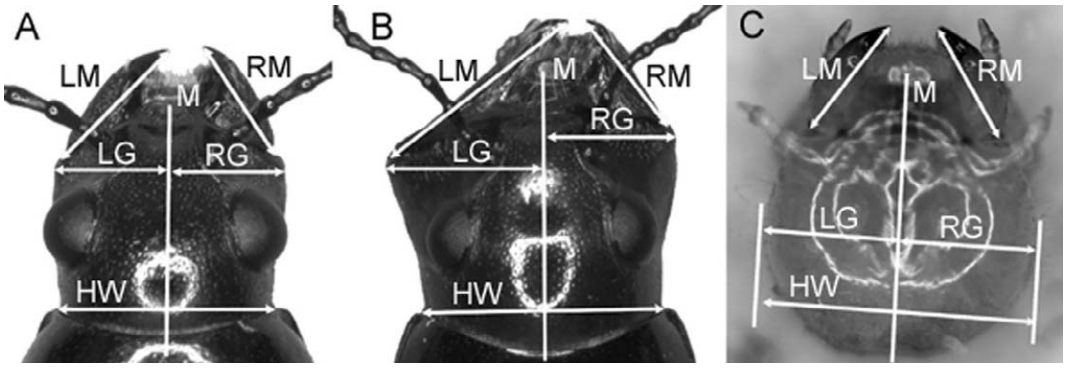


Fig. 1. Morphological traits of *Doubledaya bucculenta* heads and mouthparts. **(A)** dorsal view of an adult male's head; **(B)** dorsal view of an adult female's head; **(C)** dorsal view of the head of a larva. HW, head width; LM, left mandibular length; RM, right mandibular length; LG, left genal width; RG, right genal width; M, midline.

host bamboo culms, and deposit single eggs into the cavities of internodes via the holes (W. T., unpublished data). The males uphold their head and strike others with the head and mandibles in a hammer-like motion in male-to-male combat and mating (W. T., personal observation). Each larva completes its development in the single cavity of an internode (Hayashi, 1974). Larvae pupate at fourth to sixth instars in laboratory (W. T., unpublished data).

In this study, to determine the asymmetry types of head morphology and the relationship of the asymmetric degrees and absolute measurements of mandibles and genae to the body size in *D. bucculenta*, we measured the mandibular length, genal width, elytral length, body length, and head capsule width in larvae, adult females, and males. We also studied the oviposition preference of bamboo internodes in different-sized females, and the size relationship between bamboo internodes and the adults in them, as adult females exhibit a marked DA in their mandibles, which they use to bore a hole into the internode wall at oviposition. The latter study reveals which internode traits determine oviposition preference. Consequently, we can discuss the function of DA of female mandibles through differences in female body size related to the degree of DA of head morphology, as well as the oviposition preference for bamboo internodes.

MATERIALS AND METHODS

Head morphology

D. bucculenta adults were collected and sexed at three *P. simonii* patches of 3.03, 0.20, and 0.02 ha in Takanabe Town, Miyazaki Pref. [32°6′N, 131°31′E] in May 2006, and the third and fourth instar larvae, as determined by head capsule width, were taken from dead *P. simonii* culms in Kawaminami Town, Miyazaki Pref. [32°9′N, 131°29′E] on 28 and 29 November 2008. Body and elytral lengths of adults were determined to the nearest 0.05 mm using slide calipers. In addition, mandibular length, genal width, and head width were measured using images obtained using a digital microscope, VHX-200 (Keyence) (Fig. 1). The asymmetry index (AI) was calculated as $\{(R - L) \times 100\} / (R + L)$, where R and L were lengths of traits on the right and left sides, respectively.

Selection of *P. simonii* internodes for oviposition

Bamboo internodes were taken from more than 20 *P. simonii* culms at the site in Kawaminami in May 2007, and classified into four groups according to the central diameter; classes 1 to 4 for internodes < 12.0 mm, 12.0 to 16.0 mm, 16.0 to 21.5 mm, and 21.5 to 30.0 mm diameter, respectively. Four internodes randomly chosen from each of the four classes were set up vertically, without contacting each other, on a styrene foam block, 15.5 × 17.5 cm and 12 cm tall, with four holes in transparent plastic containers, 36 × 21 cm at the bottom, 40 × 24 cm at the top and 27 cm tall. The nearest distance between internodes was 8.5 cm. Lengths of the inter-

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nodes differed among the four classes (one-way analysis of variance, $F_{3, 88} = 14.22$, $P < 0.0001$) (mean ± SE (cm) = 19.0 ± 1.2c, 24.1 ± 1.2b, 23.5 ± 1.2b, and 30.1 ± 1.2a for classes 1 to 4, respectively; means followed by the same letters indicate no difference at the 5% level by the Bonferroni method). As the length of internodes correlated with the central diameter (see results), we used the central diameter as an indicator of internodal size. Sixteen adult females with an elytral length ranging from 7.53 to 15.74 mm collected in Kawaminami in May 2007 were placed individually in the center of the top of the block at the same distance from the four internodes. When the female finished or stopped the first ovipositional behavior at an internode, the class of the internode she selected, and the presence or absence of an egg were recorded.

Size relationships between bamboo internodes and emerging adults

D. bucculenta adults were collected from the cavities of *P. simonii* internodes at the site in Takanabe between 19 and 24 September 2006. Elytral lengths of adults as well as the lengths and central diameters of culm rings of the internodes that harbored them were measured to the nearest 0.05 mm with slide calipers. We calculated the outer surface area of the internodes as π × central diameter × length.

To determine the relationships of the outer surface area of the internode to the length, diameter, woody tissue thickness, and inner surface area, five dead culms with *D. bucculenta* ovipositional marks were sampled in the same *P. simonii* patches at the site in Takanabe, and all 76 internodes were measured for length, central diameter, and woody tissue thickness on 27 March 2009. The data were also used to determine the relationship between the diameter and woody tissue thickness of internodes.

Statistical analysis

Sexual differences in elytral length, body length, and the AI value were compared using the t-test or Welch t-test after comparing their variances by F-test. Three types of asymmetries of DA, FA, and AS are discriminated by the mean and variation of the difference between right-sided and left-sided measurements; mean = 0 and variation = normal distributed for FA, mean ≠ 0 and variation = normal distributed for DA, and mean = 0 and variation = platykurtic or bimodal for AS (Palmer, 2005). When three types of asymmetries were discriminated using the AI values, the frequency distribution of the AI values with mean ≠ 0 and variation = 0 indicated an extreme DA. Thus, when the observed frequency distribution had smaller variance than normal distribution, we judged that the trait in question was DA. The t-test and Shapiro-Wilk normality test were used to determine whether or not the AI values had a mean of zero, and whether they showed normal distribution, respectively. When they did not show normal distribution, the 95% confidence intervals (CI) were given by percentile bootstrap method (1000 replicates) to determine whether or not the AI values had a mean of zero (Christie, 2004).

Pearson's correlation coefficient and the ordinary least squares (OLS) method were used to determine the relationship between two variables. Allometric equation, $y = bx^a$, was used to express relationships of mandible and genal length (y) to elytral length or larval head capsule width (x). Allometric exponent (a) and coefficient (b) were estimated by OLS and the reduced major axis (RMA) method (Sokal and Rohlf, 1995). When the allometric exponent (a) is significantly more than unity, the allometry is referred to as "positive" and indicates that the ratio of y to x increases with increasing x, because the equation is transformed to $y/x = bx^{a-1}$. Similarly, the allometry is "negative" when the allometric exponent (a) is significantly less than unity. Analysis of covariance (ANCOVA) with outer surface area of the internode as a covariate was used to compare elytral length between the sexes. An ordinal logistic regression analysis was used to explain the probability of a female selecting an internode as a reproductive resource and the probability of successful oviposition into an internode by female body size and internode class. Calculations were performed using JMP8.0 (SAS Institute 2008).

RESULTS

Head morphology

There was a significant difference in elytral length between males (mean ± SD = 11.06 ± 2.51 mm, range = 6.30 to 16.46 mm, n = 50) and females (12.17 ± 2.27 mm, range = 7.38 to 17.01 mm, n = 48) ($t_{96} = -2.276$, $P = 0.025$), but no difference in body length between the sexes (16.89 ± 3.49 mm, range = 9.10 to 23.30 mm, n = 38 for males; 17.03 ± 3.04 mm, range = 10.10 to 23.10 mm n = 48 for females) ($t_{84} = -0.188$, $P = 0.852$). A significant positive correlation was observed between elytral length and body length in each sex ($r = 0.987$, $P < 0.0001$ for males; $r = 0.967$, $P < 0.0001$ for females). The results indicate that the difference in elytral length directly reflects the difference in adult body size.

The left mandible and gena in each adult female were longer than the right mandible and gena, respectively, indicating distinctive DA (Shapiro-Wilk normality test, $W = 0.93$, $P = 0.006$; 95% CI = –25.85 to –25.19 for AI values of mandibles; Shapiro-Wilk normality test, $W = 0.98$, $P = 0.748$; t-test, $t_{47} = -26.98$, $P < 0.001$ for mean = 0 for genae) (Table 2, Fig. 2). In each male adult, the left mandible was longer than the right (DA) (Shapiro-Wilk normality test, $W = 0.93$, $P = 0.006$; 95% CI = –7.14 to –6.05), but there was no dif-

Table 2. Asymmetry index values of mandibles and genae in relation to body size of *Doubledaya bucculenta*. M, mandibular length; G, genal width. AI, asymmetry index, is calculated as {(R – L) × 100} / (R + L), where R and L are lengths or widths of traits on the right and the left sides, respectively. Slope and *y*-intercept were given by linear regression, OLS, of AI value against body size that was expressed by elytral length for adults and head width for larvae. All values are the mean ± SE. [a]n.s. = not significant. [b]95% CI of mean was obtained by bootstrap method.

Developmental stage/sex (n = no. examined)	Trait	AI value	*P* value of Shapiro-Wilk test[a]	*P* value of t-test (mean = 0)[a] or 95% CI of mean[b]	Slope	*P*[a]	*y*-intercept	*P*[a]	R^2
Adult male (n = 50)	M	–6.60 ± 0.27	0.006	–7.14 to –6.05	0.00 ± 0.11	n.s.	–6.64 ± 1.25	< 0.001	< 0.001
	G	–0.20 ± 0.39	n.s.	0.619	0.05 ± 0.16	n.s.	–0.79 ± 1.78	n.s.	0.002
Adult female (n = 48)	M	–25.53 ± 0.17	0.006	–25.85 to –25.19	0.08 ± 0.08	n.s.	–26.50 ± 0.95	< 0.001	0.023
	G	–7.77 ± 0.29	n.s.	< 0.001	0.20 ± 0.13	n.s.	–10.15 ± 1.57	< 0.001	0.049
Larva (n = 15)	M	–0.21 ± 0.43	< 0.001	–0.87 to 0.71	–2.77 ± 2.75	n.s.	4.09 ± 4.31	n.s.	0.072
	G	0.42 ± 0.68	n.s.	n.s.	–2.22 ± 4.44	n.s.	3.87 ± 6.94	n.s.	0.019

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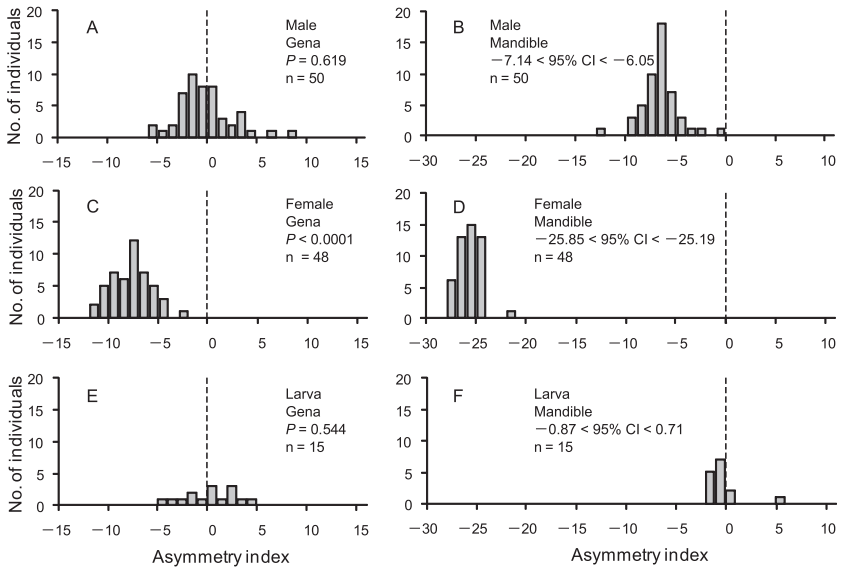


Fig. 2. Frequency distributions of asymmetry index (AI) values of mandibles and genae in *Doubledaya bucculenta* adults and larvae. AI value was calculated as {(R – L) × 100} / (R + L), where R and L are lengths of traits on the right and the left sides, respectively. The *P*-value shows the probability at which data follows the null hypothesis of asymmetry index = 0. The 95% confidence interval of mean (95% CI) was obtained by bootstrap method. **(A)** genal width of an adult male; **(B)** mandibular length of an adult male; **(C)** genal width of an adult female; **(D)** mandibular length of an adult female; **(E)** genal width of a larva; **(F)** mandibular length of a larva.

Table 3. Relationships of head width, mandibular length, and genal width to body size of *Doubledaya bucculenta* adults and larvae. All values are mean ± SE. Allometric exponent and coefficient indicate the slope and *y*-intercept in linear regression of $\log_{10}$-transformed length of traits in question against $\log_{10}$-transformed body size that is substituted by elytral length for adults and head width for larvae. [a]HW, head width; LM, left mandibular length; RM, right mandibular length; LG, left genal width; RG, right genal width. [b]Allometric exponents obtained by OLS and RMA are shown in front of and in parentheses, respectively. [c]P_1 and P_2 indicate the probabilities at which allometric exponent is equal to 0.0 and 1.0, respectively. P_3 also indicates the probability at which allometric coefficient is equal to 0.0. $^*P < 0.001$, n.s. = not significant. [d]n = 43.

Developmental stage/sex (n = no. examined)	Trait[a]	Length (mm)	Allometric exponent[b]	P_1[c]	P_2[c]	Allometric coefficient	P_3[c]	r
Adult male (n = 50)	HW[d]	2.13 ± 0.06	0.76 ± 0.02 (0.99)	*	*	–0.46 ± 0.02	*	0.98
	LM	1.46 ± 0.04	0.78 ± 0.03 (0.97)	*	*	–0.64 ± 0.03	*	0.97
	RM	1.28 ± 0.03	0.78 ± 0.03 (0.97)	*	*	–0.71 ± 0.03	*	0.96
	LG	1.16 ± 0.03	0.77 ± 0.02 (0.98)	*	*	–0.74 ± 0.02	*	0.98
	RG	1.15 ± 0.03	0.78 ± 0.03 (0.98)	*	*	–0.75 ± 0.03	*	0.99
Adult female (n = 48)	HW	2.87 ± 0.07	0.85 ± 0.03 (0.98)	*	*	–0.46 ± 0.03	*	0.98
	LM	2.72 ± 0.06	0.86 ± 0.03 (0.97)	*	*	–0.50 ± 0.03	*	0.97
	RM	1.61 ± 0.04	0.88 ± 0.03 (0.97)	*	*	–0.75 ± 0.03	*	0.97
	LG	1.86 ± 0.04	0.83 ± 0.03 (0.97)	*	*	–0.63 ± 0.03	*	0.96
	RG	1.60 ± 0.04	0.88 ± 0.03 (0.97)	*	*	–0.75 ± 0.03	*	0.96
Larva (n = 15)	LM	0.73 ± 0.02	1.02 ± 0.10 (0.94)	*	n.s.	–0.33 ± 0.02	*	0.93
	RM	0.73 ± 0.02	0.93 ± 0.14 (0.89)	*	n.s.	–0.32 ± 0.03	*	0.87
	LG	0.77 ± 0.02	1.03 ± 0.07 (0.97)	*	n.s.	–0.31 ± 0.01	*	0.97
	RG	0.78 ± 0.02	0.97 ± 0.07 (0.97)	*	n.s.	–0.29 ± 0.01	*	0.97

ference in genal width between the sides (FA) (Shapiro-Wilk normality test, W = 0.97, $P = 0.160$; t-test, $t_{49} = -0.50$, $P = 0.619$ for mean = 0) (Table 2, Fig. 2). Larval mandibular length exhibited no clear asymmetry patterns (Shapiro-Wilk normality test, W = 0.69, $P < 0.001$; 95% CI = –0.87 to 0.71) but genal width exhibited FA patterns (Shapiro-Wilk normality test, W = 0.96, $P = 0.676$; t-test, $t_{14} = 0.62$, $P = 0.544$ for mean = 0; Table 2, Fig. 2).

Male and female adults and larvae exhibited a significant, positive correlation between body size, which was substituted by elytral length or head width, and mandibular length (Table 3). They also showed a significant, positive correlation between body size and genal width on both sides (Table 3). However, there were no significant correlations between body size and the AI values of mandibular length and genal width (Table 2). The mean and variance of AI values of mandibles and genae were significantly smaller in adult females than males (F-test, $F_{49, 47} = 2.56$, $P = 0.002$ for mandibles; $F_{49, 47} = 1.88$, $P = 0.032$ for genae; Welch t-test, $t_{1, 82.7} = 58.83$, $P < 0.0001$ for mandibles; $t_{1, 89.7} = 15.71$, $P < 0.0001$ for genae) (Table 2, variance = sample size × SE). The allometries of the traits of males and females estimated by OLS and RMA were negative (OLS, allometric exponent < 1, $P < 0.001$, Table 3), whereas those of larvae estimated by OLS were not significantly different from 1.0 (OLS, allometric exponent < 1, $P > 0.05$, Table 3).

Selection of *P. simonii* internodes for oviposition

Thirteen females finished ovipositing, but the three others stopped. A logistic regression analysis showed that the probability at which a female selected different classes of internodes as an ovipositional resource varied depending on female body size (ordinal logistic regression analysis, $\chi^2_1 = 7.74$, $P = 0.005$; Fig. 3A). Class 1, 2, 3 and 4 internodes were selected most often by females with an elytral length of 7.53 to 7.73mm, 7.74 to 12.49 mm, 12.50 to 13.98 mm and 13.99 to 15.74 mm, respectively.

The estimated density function of the probability at which a female actually deposited an egg into different classes of internodes also varied depending on female body size (ordinal logistic regression analysis, $\chi^2_1 = 9.38$, $P = 0.002$; Fig. 3B). Class 1, 2, 3, and 4 internodes were selected most often by females with an elytral length of 7.53 to 9.36 mm, 9.37 to 13.34 mm, 13.35 to 14.81 mm and 14.82 to 15.74 mm, respectively.

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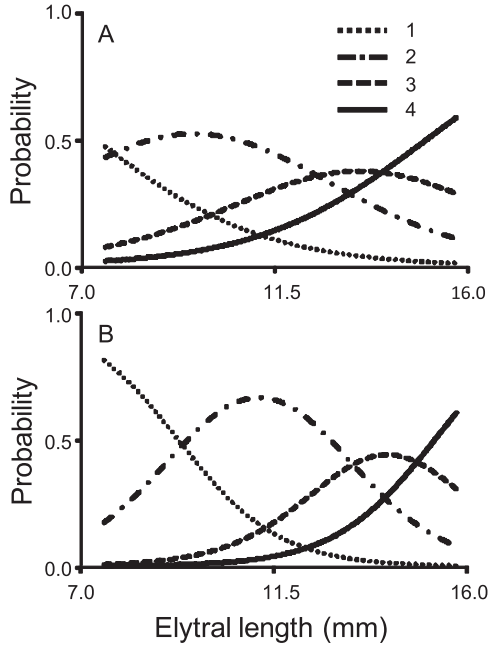


Fig. 3. Probability of oviposition in *Pleioblastus simonii* internodes by *Doubledaya bucculenta* females. **(A)** probability at which a female of specified elytral length selected an internode of one of four different size classes as an ovipositional resource. **(B)** probability at which a female of specified elytral length deposited an egg into an internode of one of four different size classes. Classes 1 to 4 represent four groups of internodes with a central diameter of less than 12 mm, 12.0 to 16.0 mm, 16.0 to 21.5 mm and 21.5 to 30 mm, respectively.

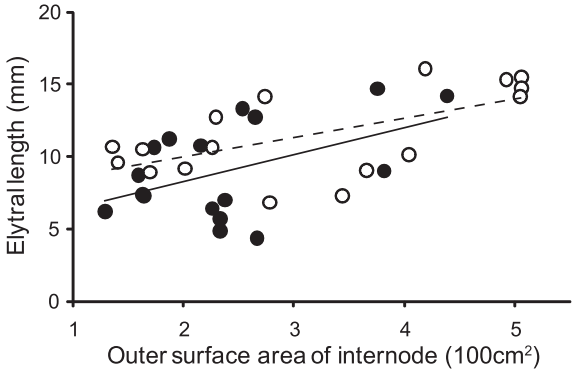


Fig. 4. Size relationships between *Doubledaya bucculenta* adults and the *Pleioblastus simonii* internodes where they developed. Black dots with a solid regression line and white dots with a dashed regression line represent males and females, respectively. y = 4.51 + 2.02 x, P = 0.024, for males, y = 7.30 + 1.33 x, P = 0.001, for females.

Size relationships between adults and bamboo internodes

A total of 33 adults were collected from bamboo culms. They occupied cavities of different internodes singly. Adult body size correlated positively with the outer surface area of the internode where it developed (r = 0.558, P = 0.025, n = 16 for males; r = 0.607, P = 0.010, n = 17 for females; Fig. 4). The relationship between body size and the outer surface area of the internode did not differ between the sexes (ANCOVA, $F_{1,29}$ = 1.05, P = 0.313 for sex; $F_{1,29}$ = 14. 53, P = 0.0006 for outer surface area, $F_{1,29}$ = 0.61, P = 0.443 for the interaction).

The outer surface area of the internode correlated positively with length (r = 0.57, P < 0.0001), central diameter (r = 0.99, P < 0.0001), woody tissue thickness (r = 0.95, P < 0.0001), and inner surface area (r = 0.99, P < 0.0001). The central diameter correlated positively with woody tissue thickness (r = 0.94, P < 0.0001).

DISCUSSION

The heads of *D. bucculenta* adults showed distinct sexual dimorphism; marked left-DA in female mandibular length and genal width vs. left-DA in male mandibular length, which was the first report, and FA in male genal width (Table 2, Fig. 2). In contrast, the larval mandibles in late instars exhibited no clear asymmetry patterns in length, and their genal width showed an FA pattern (Table 2, Fig. 2). A female-enhanced asymmetry of mandibles and genae has been found in all species of the genus *Doubledaya* (Villiers, 1945; Wegrzynowicz, 2002). This is different from marked asymmetric mandibles reported to date, because the asymmetry is exhibited by males or both sexes (Hori, 1993; Inoda et al., 2003; Miller and Wheeler, 2005; Hoso et al., 2007). In such cases, the asymmetry is reported to be closely linked to male-to-male conflict or feeding.

Mandibles and genae are connected with muscles in insects. Adductor and abductor mandibularis muscles are attached to the basal part of the mandible and inside wall of the head capsule. Contraction of adductor mandibularis muscles produces the force to chew. In beetles that bore a hard substrate such as woody tissue, adductor mandibularis muscles occupy a large amount of the head capsule (Morimoto and Hayashi, 1986). Therefore, the enlarged left gena of *D. bucculenta* female is related closely to the function of the enlarged left mandible.

Female and male adults of *D. bucculenta* cut the bamboo fibers to exit from internode cavities where they developed. They consume foods on internode surface using the maxillae. Adult females cut the bamboo fibers with the mandibles again to gnaw a small hole through the internode wall and deposit an egg in, whereas the males use their mandibles in a hammer-like manner in male-to-male combat and mating (W. T., personal observation). Larvae do not chew the inner wall of the internode with the mandibles, but likely consume foods on the surface of the inner wall using maxillae (W. T., personal observation). Therefore the degree of asymmetry of mandibles and genae varies depending on the frequency of cutting bamboo fibers among larvae, male, and female adults, suggesting that the DA of *D. bucculenta* mandibles and genae may be linked to the cutting of bamboo fibers. This explanation may also be applied to the DA of larval mandibles of the stag beetle *Prosopocoilus inclinatus*, which cut wood fibers using the mandibles (Okada et al., 2008).

Bamboos have harder woody tissue of internodes than do herbaceous plants. This suggests the hypothesis that between-species difference in the degree of DA of female mandibles and genae varies depending on the hardness of host plant tissues into which the females bore holes.

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Although marked DA of female mandibles and genae has been reported in all species of the genus *Doubledaya*, their host plants have been unknown except for bamboos of *D. bucculenta* (Villiers, 1945; Wegrzynowicz, 2002; Table 1). In other genera of the tribe Languriini that comprises the genus *Doubledaya*, *Anadastus pulchelloides* Nakane, which lives on the gramineous weed *Arundinella hirta* (Thunb.) Tanaka, show low DA of female mandibles (mean of AI values ± SE = –2.09 ± 0.31, n = 14), and no clear asymmetry patterns of female genae (–0.77 ± 0.28, n = 14) (W. T., unpublished data). That is true for *Languriomorpha lewisii* female (host plant = the fern *Pteris wallichiana* Ag. (Sasaoka, 2009), mean of AI values ± SE = –2.67 ± 0.39, n = 17 for female mandibles; –0.05 ± 0.36, n = 17 for female genae) (W. T., unpublished data). DA of female mandibles and genae may be adapted for the tissue hardness of host plants.

The variance of the AI values in mandibular length was smaller in female adults than in males in *D. bucculenta* (Table 2). This was also true for the genal width. Both the small difference in the AI value and the marked directional asymmetry of the female mandibles may be a result of stronger selection pressure in females than in males. This may suggest that additive genetic variance is almost depleted.

Internodes that a given-sized *D. bucculenta* female chose for oviposition showed a larger range than those in which she actually oviposited, because females, especially small females, could not always lay eggs successfully in the internodes they selected, due to incomplete holes in larger internodes (Fig. 3). Consequently, larger females oviposited into large-diameter internodes, and smaller females into small-diameter internodes (Fig. 3). This assortative oviposition may divide one population into different-sized groups as the result of a positive relationship between internode diameter and emerging adult size (Fig. 4), although in general, larger females lay more eggs than smaller females (Honěk, 1993), and larger males are often superior to smaller ones in competition (Gullan and Cranston, 2005).

Large diameter of internode means low curvature of internode surface (= 1/radius of internode) and thick woody tissue through which females gnaw a hole. Large females have larger but less asymmetrical mandibles than small females, although the positive correlation between female body size and the AI value of mandibles was not statistically significant. Considering that large mandibles are necessary to make a hole in thick woody tissue of internode, DA of mandibles may be adapted to the rounded surface of hard internodes.

Mandibular length and genal width in *D. bucculenta* female and male adults showed negative allometries (Table 3). Sexually selected traits frequently show positive allometries; as, for example, in male structures used as signaling devices and weapons (Huxley, 1931; Green, 1992; Petrie, 1992; Ryan and Keddy-Hector, 1992; Emlen and Nijhout, 2000; Tomkins et al., 2005; Kodric-Brown et al., 2006). Therefore, it is considered that the mandible and gena of *D. bucculenta* adults are not sexually selected traits, although sexually selected traits sometimes do show negative allometries (Eberhard, 2002; Bonduriansky, 2007). More observations of intra- and intersexual behavior are needed.

The directions of asymmetry of female mandibles and genae examined were fixed to left within the study population of *D. bucculenta*. Left-DA of female mandibles and genae has been reported for four other conspecific populations (Lewis, 1884; Toki, 2009). That would provide another conditional evidence for functional advantages of the direction of asymmetry in *D. bucculenta* female. The common direction of mandibular and genal asymmetry in all species of the genus *Doubledaya* (Villiers, 1945) suggests the directions of asymmetry in *D. bucculenta* to be under the phylogenetic constraint. Interspecific comparative studies on behavior will be necessary to better understand the significance of the asymmetry and its direction in *D. bucculenta*.

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