

Allometry of male genitalia in a lepidopteran species, *Ostrinia latipennis* (Lepidoptera: Crambidae)

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(Received 6 December 2002; Accepted 31 March 2003)

Abstract

In species of several insect orders and spiders, it has been shown that the size of male genitalia relative to body size decreases as the body becomes larger (negative allometry), while the relative size of other morphological traits tends to be constant. Such a contrast between genital and somatic traits suggests stabilizing sexual selection on male genitalia: males with small or large genitalia are prone to fail to inseminate females due to incompatibility of their genitalia. In the present study, we tested the contrast between genital and somatic traits for males of a lepidopteran insect, *Ostrinia latipennis*. We examined allometry of five genital and 11 somatic traits for each of three local populations of *O. latipennis*. Of the 15 allometric slopes for genital traits, 14 showed significantly negative allometry, whereas none of the 33 slopes for somatic traits represented negative allometry. These results showed that the size of male genitalia in *O. latipennis* is more stable than the size of somatic traits against changes in body size. This study supports Eberhard et al.'s (1998) hypothesis which states that the low genital allometry in insects and spiders is caused by sexual selection. Based on currently available information on genital morphology and sexual communication in *O. latipennis*, it seems unlikely that the lock-and-key hypothesis is responsible for the stable genital size in this species.

Key words: Allometry; male genitalia; stabilizing selection; Lepidoptera; *Ostrinia latipennis*

INTRODUCTION

Allometry, i.e., the scaling relationship between the size of a given morphological trait and body size at a particular developmental stage of an organism, has been focused on in studies of morphological evolution. The observed allometric slope (a slope in log-log regression on an indicator of body size) is presumably a consequence of selection that favors one slope over the others (Eberhard et al., 1998). In male animals, secondary sexual traits which are probably under sexual selection tend to become relatively larger in individuals with a larger body, resulting in positive allometry (allometric slopes being larger than 1.0) (e.g., Alatalo et al., 1988; Petrie, 1988, 1992; Green, 1992; Emlen and Nijhout, 2000). In contrast, ordinary morphological traits probably not under sexual selection show isometry (allometric slopes around 1.0) (Harvey and Pagel, 1991).

Eberhard et al. (1998) examined the allometry of the sizes of male genitalia and other body parts in 20 species of insects (including those belonging to Coleoptera, Diptera, Hymenoptera, Hemiptera, Dermaptera and Odonata) and spiders. They found that allometric slopes for male genitalia were consistently lower than 1.0 and lower than the slopes for the other body parts. Based on these findings, they suggested that within a species sexual selection favors males with genitalia of standard sizes. Several studies on beetles, dipterans and a spider have similarly detected negative allometry for male genital size (Wheeler et al., 1993; Palestini et al., 2000; Schmitz et al., 2000; Uhl and Vollrath, 2000; Iwahashi, 2001; Iwahashi and Routhier, 2001; Tatsuta et al., 2001). The lower allometry for male genital size appears to be common among insects and spiders. To date, however, studies on genital allometry have been concentrated on beetles, dipterans and spiders (27 out of 31 species examined

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belong to these three groups). It is thus premature to conclude that the negative allometry of male genitalia is common in insects, without examining other major taxa.

We examined the allometry of genital and non-genital morphological traits of a crambid moth, the Far Eastern knotweed borer, *Ostrinia latipennis* (Warren). This is the first study examining allometry of genital size in Lepidoptera. We discuss the significance of the genital allometry in *O. latipennis* along with hypotheses on the evolution of animal genitalia.

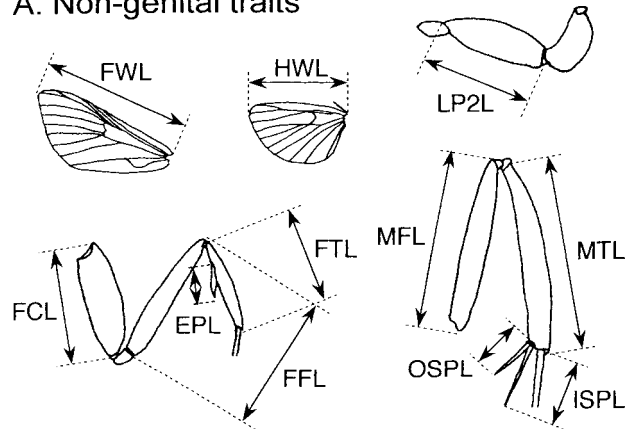
MATERIALS AND METHODS

Insects and morphological measurements. *Ostrinia latipennis* (Warren) (Crambidae: Pyraustinae) is distributed in northern Far East Asia including northeastern Japan (Mutuura and Munroe, 1970; Ohno, 1998). Larvae of *O. latipennis* feed mainly on knotweeds, *Reynoutria sachalinensis* and *R. japonica* (Polygonaceae) (Ishikawa et al., 1999; Ohno, 2000). To examine the geographic variation in male morphology among seven local populations of *O. latipennis*, Ohno (1998) conducted multivariate analyses on 16 morphological traits (11 somatic and five genital). Of these seven populations, three (Otoineppu-Vil., Hokkaido Is., 44.7°N 142.3°E; Tazawako-Town, Akita-Pref., Honshu Is., 39.8°N 140.8°E; Unazuki-Town, Toyama-Pref., Honshu Is., 36.9°N 137.6°E), with sufficient sample size (over 30 for each population), were used for the present analyses.

The 11 somatic traits analyzed in the present study were the lengths of the following body parts: fore wing, hind wing, fore coxa, fore femur, fore tibia, mid femur, mid tibia, epiphysis (leaf-shaped projection on the fore tibia), outer mid-tibial spur, inner mid-tibial spur and the 2nd segment of the labial palpus (Fig. 1). The five genital traits analyzed included four parts of the grasping organ, i.e., valva length, sacculus length, harpe length and clasper width, and one part of the intromittent organ, aedeagus length (Fig. 1). The sizes of the traits (in mm) are shown in Table 1. See Ohno (1998) for further details on insect collection and measurement acquisition.

Several previous studies on genital allometry used a single somatic trait as the indicator of body size (e.g., width of pronotum or thorax). Such a

A. Non-genital traits



B. Genital traits

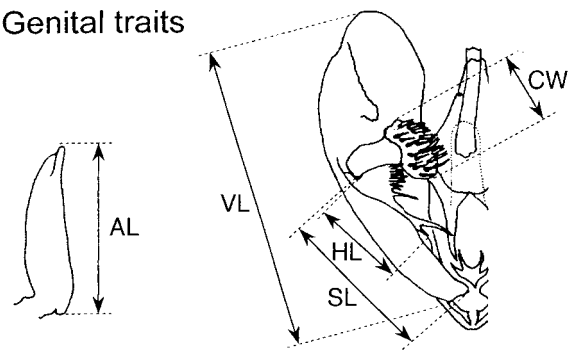


Fig. 1. Measurements of somatic and genital morphology of *Ostrinia latipennis* (redrawn from Ohno, 1998). A, non-genital traits. FWL, forewing length; HWL, hindwing length; FCL, fore coxa length; FFL, fore femur length; FTL, fore tibia length; MFL, mid femur length; MTL, mid tibia length; EPL, epiphysis length; OSPL, outer mid-tibial spur length; ISPL, inner mid-tibial spur length; LP2L, labial palpus 2nd segment length. B, genital traits. VL, valva length; SL, sacculus length; HL, harpe length; CW, clasper width; AL, aedeagus length. The overall body size was represented by the first principal component (PC1) score based on the 16 traits (see Materials and Methods) where $PC1 = 0.095FWL + 0.074HWL + 0.262FCL + 0.333FFL + 0.284FTL + 0.379MFL + 0.411MTL + 0.207EPL + 0.225OSPL + 0.419ISPL + 0.315LP2L + 0.131VL + 0.097SL + 0.090HL + 0.040CW + 0.094AL$.

body-size indicator may have a closer ontogenetic and functional relationship with other somatic traits than with genital traits, and the use of a different body-size indicator may give rise to different results (Green, 1999). Thus, we used the principal component 1 (PC1) as an overall measure for body size. The PC1 score was calculated from the variance-covariance matrix of the raw measurements on the 16 body parts. In calculations of the PC1 scores, the constant was set at zero to prevent

Table 1. Allometric slopes and other features of phenotypic variation for 16 morphometric traits of *Ostrinia latipennis* males from three localities (Otoineppu, Tazawako and Unazuki) in Japan^a

Trait category	Mean (mm)	Otoineppu (n=35)			Tazawako (n=38)			Unazuki (n=34)			
		Slope	CV	r	Slope	CV	r	Slope	CV	r	
Somatic	Fore wing length	14.22	0.94 ns	0.91*	1.13 ns	6.64	0.97*	1.13 ns	5.46	0.95*	1.78
	Hind wing length	10.68	0.95 ns	0.90*	1.15 ns	6.84	0.95*	1.27*	6.17	0.94*	2.13
	Fore coxa length	2.11	1.06 ns	0.96*	1.12 ns	6.70	0.95*	1.27 ns	6.46	0.90*	2.78
	Fore femur length	2.84	0.99 ns	0.95*	1.10 ns	6.43	0.97*	1.10 ns	5.39	0.93*	1.96
	Fore tibia length	1.35	1.04 ns	0.89*	1.33*	8.09	0.94*	1.21 ns	6.19	0.89*	2.87
	Mid femur length	3.33	0.97 ns	0.96*	1.07 ns	6.20	0.98*	1.12 ns	5.36	0.96*	1.54
	Mid tibia length	3.50	1.02 ns	0.93*	1.15 ns	6.92	0.94*	1.17 ns	5.93	0.91*	2.52
	Epiphysis length	0.64	0.88 ns	0.85*	1.04 ns	7.47	0.81*	1.01 ns	6.53	0.72*	4.53
	Outer mid-tibial spur length	0.75	1.46 ns	0.69*	1.20 ns	9.00	0.74*	0.41 ns	8.40	0.25 ns	—
	Inner mid-tibial spur length	1.26	1.22 ns	0.83*	0.83 ns	6.25	0.74*	1.10 ns	7.03	0.73*	4.83
Genital	Labial palpus 2nd seg. length	0.93	1.09 ns	0.82*	0.96 ns	7.19	0.76*	0.80 ns	5.83	0.62*	4.59
	Valva length	2.28	0.48*	0.76*	0.46*	3.36	0.78*	0.37*	2.82	0.60*	2.25
	Sacculus length	1.21	0.36*	0.65*	0.42*	3.38	0.72*	0.38*	3.08	0.57*	2.54
	Harpe length	0.75	0.33*	0.45*	0.56*	5.27	0.61*	0.29*	4.70	0.29 ns	—
	Clasper width	0.51	0.39*	0.62*	0.01*	3.77	0.02 ns	0.17*	6.56	0.14 ns	—
	Aedeagus length	1.21	0.57*	0.75*	0.38*	4.18	0.52*	0.59 ns	4.50	0.59*	3.62

^a Slope (SE): slope of regression line of a trait on body size (both variables log-transformed). CV: coefficients of variation (standard deviation divided by the mean) calculated for non-transformed variable. *r*: Pearson product-moment correlation coefficient between a trait and body size. CV': a measure of the degree of dispersion of data points around the regression line, expressed as $CV(1-r^2)^{1/2}$. CV' was not calculated when *r* was insignificant. As an indicator of body size, the principal component 1 score based on the variance-covariance matrix of the 16 traits was used. Significance tests for regression slopes and correlation coefficients were done against the null hypotheses of slope=1 and of *r*=0, respectively, where the group-wise error rate was adjusted at 0.05 by the sequential Bonferroni method (Rice, 1989) (*, $p < 0.05$; ns, no significance).

negative PC1 values, which allowed log-transformation of the scores.

Estimation of allometric slope and other features of morphological variation. For each trait, the allometric slope was estimated by linear regression analysis of the \log_{10} -transformed value of the trait on the \log_{10} -transformed PC1 score. Such an estimation of slopes has been commonly used in studies of allometry (Gould, 1966), and is unaffected by differences in the unit of measurement among traits (Smith, 1980). We used the type I (ordinary least square, OLS) regression analysis (Eberhard et al., 1998, 1999; Cuervo and Møller, 2001). Green (1999) argued that, for the study of allometry, the type II (e.g., reduced major axis, RMA) regression method is more appropriate than the OLS regression, because the OLS method assumes that the independent variable is measured without error (Sokal and Rohlf, 1995). However, the use of RMA regression was inapplicable for the present data because a few correlation coefficients, which are used in calculating the slope of RMA regression, were not significant (Table 1; see Eberhard et al., 1999; Cuervo and Møller, 2001). The estimates of the regression slopes were tested against the null hypothesis of isometry (slope=1.0) by *t*-tests. Since allometric relationships may vary among populations (Wilkinson, 1993; Akimoto et al., 1994), we compared the regression lines of the three populations for each of the 16 traits by the analysis of covariance (ANCOVA; Sokal and Rohlf, 1995).

Several studies regarding the evolution of trait sizes in animals have utilized the coefficient of variation (CV) (e.g., Pomiankowski and Møller, 1995; Arnqvist and Thornhill, 1998) as well as the allometric slope. The difference in CV values among traits is affected by the degree of dispersion of data points around the allometric line, in addition to the allometric slope (see Fig. 1 in Eberhard et al., 1998). The allometric slope is considered to reflect a design feature of an organism, while the degree of dispersion around the line is affected by various genetic and environmental factors (Eberhard et al., 1998). To estimate the degree of dispersion of points around the line, we calculated the CV' (the coefficient of variation when a variable representing the body size is held constant; see Eberhard et al., 1998). CV' for a trait is expressed as $CV \times (1 - r^2)^{1/2}$ where *r* is the correlation coefficient

of the trait with the body size. Because CV' is invalid when *r* is not significant (Eberhard et al., 1998; Cuervo and Møller, 2001), we also calculated another measure of the degree of dispersion of points, i.e., the standard error of estimate (SEE, the square root of the residual mean square from the regression line; see Cuervo and Møller, 2001). SEE is unaffected by *r*, but has the disadvantage of not being dimensionless (Eberhard et al., 1998).

The allometric slope, CV, CV' and SEE were respectively compared between trait categories (genital vs. somatic) by the Mann-Whitney *U*-test within each population.

RESULTS

The first principal component (PC1) explained 68.6% of the total variance, and all of the 16 traits had positive loading on the PC1 (the eigenvector for PC1 shown in the caption of Fig. 1). The PC1 scores were significantly differentiated among the three populations (one-way ANOVA, $p < 0.001$).

The majority of the allometric slopes for the somatic traits (31 of 33) did not significantly deviate from 1.0 (Table 1). In contrast, almost all slopes for the genital traits (14 of 15) were significantly less than 1.0 (Table 1). The slopes for genital traits were significantly lower than the slopes for somatic traits in all of the three populations (Mann-Whitney *U*-test, $p < 0.01$ for all populations).

Genital traits showed lower CV than somatic traits (Table 1), and the difference in CV between the trait categories (somatic vs. genital) was significant for all populations (Mann-Whitney *U*-test, $p < 0.01$ for Otoineppu and Tazawako, $p < 0.05$ for Unazuki). Neither of the two measures of dispersion of points around the allometric line, CV' (Table 1) and SEE (not shown), differed significantly between the trait categories in any of the populations (Mann-Whitney *U*-test, $p > 0.5$ for all populations).

ANCOVAs indicated that, for all 16 traits, the regression slopes did not vary significantly among the three populations ($p > 0.05$, *p* values were corrected by the sequential Bonferroni procedure; Rice, 1989). All but four traits (lengths of fore tibia, outer mid-tibial spur and sacculus, and clasper width) showed significant population differentiation in the intercepts of the regression lines ($p < 0.05$ with the sequential Bonferroni

correction).

DISCUSSION

Allometry of male genitalia

Male genital traits of *O. latipennis* showed negative allometry, while the allometric slopes of the somatic traits were isometric. Genital traits showed less phenotypic variation than somatic traits. The degree of dispersion of data points around the allometric lines did not differ between genital and somatic traits. These findings show that, in *O. latipennis*, 1) the size of male genitalia is more stable than that of non-genital body parts against changes in the body size, and 2) the difference in the degree of phenotypic variation between genital and somatic traits is attributed to the difference in allometric slopes (and thus difference in the design feature).

The present findings are congruent with those of previous studies that analyzed both the allometric slope and the dispersion of points around the allometric line for male genitalia and other body parts (Eberhard et al., 1998; Palestini et al., 2000), and also congruent with those of studies that examined allometric slope only (Wheeler et al., 1993; Uhl and Vollrath, 2000; Iwahashi, 2001; Iwahashi and Routhier 2001; Tatsuta et al., 2001). Since the shape of male genitalia is conspicuously diversified among taxa in insects and spiders (e.g., Eberhard, 1985), it is particularly interesting that male genital size is stable within single populations of diverse taxa. This may suggest that a common evolutionary force has stabilized the male genital size within various species of insects and spiders.

Eberhard (1985, 1996) regarded the male genitalia of animals as a copulatory courtship device that is designed to mechanically stimulate females in a specific way during the copulation, in contrast to the male ornaments that stimulate females visually. Along this concept, Eberhard et al. (1998) proposed that sexual selection can cause low allometry for male genital sizes, as follows. Females generally perceive a male's genitalia at close range by more or less precisely aligned touch, rather than visually at long range. Through the tactile channel, the female's own size is likely to directly affect her perception of the male. Then, selection for males who most effectively stimulate their mates with typical size may favor intermediate, standard sizes

of male genitalia (and thus lead to low allometric slopes). The present findings suggest that such sexual selection operates on genital size in lepidopteran insects.

Another hypothesis on the evolution of genitalia, the lock-and-key (see Shapiro and Porter, 1989), also predicts low allometric slopes for male genital sizes (Eberhard et al., 1998). Under the lock-and-key hypothesis, mechanical or sensory fit between male and female genitalia should have evolved to avoid hybridization (Eberhard, 1985), and thus genitalia of intermediate sizes are favored by stabilizing selection (Arnqvist, 1997). In *O. latipennis*, three lines of evidence suggest that species-specificity in male genital morphology does not effectively function as a precopulatory reproductive barrier against related species, and thus the lock-and-key hypothesis is unlikely to explain the lower allometry of male genitalia. First, the valva of male genitalia possesses highly spinose parts such as clasper and harpe (Fig. 1B), while the female organs that the valva touches are not specialized for receiving it (S. Ohno, pers. obs.). Second, males of *Ostrinia* moths show considerable interspecific differences in the size (Ohno, 2003a; S. Ohno, pers. obs.) and shape (Mutuura and Munroe, 1970) of genitalia, while females do not appear to express such differences (Mutuura and Munroe, 1970; Ohno, 2003a; S. Ohno, pers. obs.). These two facts suggest no apparent mechanical fit of genitalia between sexes in the genus *Ostrinia*. Third, *O. latipennis* has a sexual communication system mediated by the female sex pheromone as in other moth species (Takanashi et al., 2000), and the species specificity of sex pheromone composition in *Ostrinia* moths certainly contributes to pre-mating reproductive isolation between sympatric congeners (Ishikawa et al., 1999; Ohno, 2003b). Therefore, hybridization attempt between *O. latipennis* and its relatives is not likely to occur frequently.

Geographic variation in genital size

Among the three populations of *O. latipennis*, no traits showed geographic variation in the allometric slopes, while the intercepts of allometric lines varied geographically in the majority of traits including three genital traits, i.e., the lengths of valva, harpe and aedeagus. This suggests that the sizes of the three genital traits relative to the body size

show geographic variation. The three genital traits were significantly correlated with the PC1 scores in all populations, except for harpe length in the Unazuki population (Table 1), and the PC1 scores were significantly differentiated among the three populations. If the phenotypic correlations with the indicator of body size reflect genetic correlations (Cheverud, 1988), it is possible that the genital traits in *O. latipennis* are geographically differentiated by an indirect effect of natural selection acting on body size (the pleiotropy hypothesis for genital evolution; Mayr, 1963). However, other explanations such as direct selection acting on the genital traits and genetic drift cannot be excluded and remain to be tested.

ACKNOWLEDGEMENTS

We thank Haruki Tatsuta, National Institute of Genetics, for his advice on statistical methods. This study was supported in part by a Grant-in-Aid from the Ministry of Education, Culture, Sports, Science and Technology of Japan (No. 13460021).

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