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Limits to the exaggeration and diversification of a male sexual trait in the false blister beetle *Oedemera sexualis*

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Abstract

Differentiation in sexual traits among populations is one of the major predictions of theories of sexual selection and sexual conflict. A balance between maximizing reproductive benefits and minimizing survival costs may explain variation in sexual traits within and between populations. The false blister beetle *Oedemera sexualis* (Coleoptera: Oedemeridae) has exaggerated sexual traits, i.e., sexually dimorphic hind legs. In this study, we characterized scaling relationships in populations of *O. sexualis* to evaluate the determinants of sexual trait variation in the species. We quantified sexual dimorphism in body size and hind leg sizes in three representative populations based on distance measurements and an elliptical Fourier analysis. We found significant variation in the degree of sexual dimorphism for body and hind leg sizes among populations. In particular, differentiation in the male hind femur shape, especially the femur width, was conspicuous. Scaling relationships between male hind femur width and body size were best described by logistic models, showing that increases in male hind femur width were constrained for large individuals in all three populations. The degree of constrained growth of the hind femur width differed among populations in accordance with the population means, while the basal growth rates did not. Populations with smaller mean values for sexual traits showed more limited sexual trait exaggeration, contrary to the predictions based on resource competition among body parts. The latitudinal cline in femur widths suggests that environmental constraints on exaggeration may be responsible for sexual trait diversification in *O. sexualis*.

Key words: allometry, elliptical Fourier analysis, sexual conflict, sexual dimorphism, sexual selection

INTRODUCTION

Sexual selection is responsible for the exaggeration and incredible diversity of male sexual traits in animals (Darwin 1871, Andersson 1994). Resource allocation to these spectacular sexual traits may confer fitness benefits in terms of reproductive success (Andersson 1994). Sexual selection generating exaggerated traits often results in a steep scaling relationship with body size, such that the trait becomes disproportionately larger with increasing body size (e.g., Kodric-Brown et al. 2006, Lavine et al. 2015). Scaling relationships are often best described by a straight line using log-transformed body and sexual trait sizes. However, for sexual traits in some taxa, relationships between log-transformed variables are better described by curved, sigmoidal, or discontinuous functions (Knell 2009). Such departures from simple linear relationships (i.e., nonlinear allometric relationships) can probably be attributed to evolutionary forces that modify the scaling relationships between trait size and body size.

Nonlinear allometric relationships have frequently been found in male weapons, in which resource competition between the weapon and other body parts result in declines in allometric slopes at large body and weapon sizes (Nijhout and Emlen 1998, Knell et al. 2004). Constraints on the growth of elaborated sexual traits may be a consequence of limited resource availability (Tomkins et al. 2005, Knell et al. 2004). In holometabolous insects, competition for resources can occur among growing body parts within the pupa (Nijhout and Wheeler 1996, Moczek and Nijhout 2004). The development of a disproportionally large sexual trait is expected to constrain growth. For example, in the scarabaeid beetle *Onthophagus taurus,* there is a non-linear relationship between male horn length and body size, even when values were log-transformed; exponential horn growth is observed in relatively small males and constrained growth is observed in relatively large males (Tomkins et al. 2005). This may be explained by two non-mutually exclusive processes: (1) large weapons disproportionally increase male mating success and sexual selection favors disproportional investment in the weapon with increasing body size, and (2) resource competition between body parts in the pupal stage may be severe in large males with disproportionally large weapons, such that the growth of the weapon is constrained. This type of nonlinear allometry may also be related to the bimodal distribution of weapon size in relation to alternative mating tactics, including male-male competition by large males and sneaking by small males (e.g., Moczek and Emlen 2000). From a comparative point of view, the growth of the trait is expected to be more strongly constrained in species or populations with relatively large traits because resource competition between the trait and other body parts would be more intense (Knell et al. 2004).

Exaggerated trait expression is also constrained by survival costs (Endler 1983, Jennions et al. 2001). For example, diopsid flies that carry longer eyestalks have increased mating success (Wilkinson & Dodson 1997) but also a reduced flight ability (Swallow et al. 2000). Thus, sexually selected traits reflect a balance between natural and sexual selection (Andersson 1982, Nur and Hasson 1984). This process may be influenced by several environmental factors (e.g., habitat type, resource availability, and predation pressure); therefore, the exaggerated traits may vary depending on the precise environmental conditions, leading to the diversification of sexual traits among species and/or populations (Moczek and Nijhout 2003, Svensson et al. 2004, Miller and Emlen 2010). Natural selection is also expected to modify the scaling relationships between sexual traits and body sizes; however, few studies have examined whether and how this process influences the scaling relationships and diversification of sexual traits.

The false blister beetle *Oedemera sexualis* (Coleoptera: Oedemeridae) is an ideal model system for evaluating geographic variation in exaggerated sexual traits. The species is widely distributed, and its hind leg morphology is sexually dimorphic (Fig. 1a, b). Male hind legs are massive and function as a female-grasping apparatus, while female hind legs are slender and are used to dislodge the mounting male by dashing and kicking (Koshio et al., unpublished data, see also Burrows 2020) (Fig. 1c). Male–male combat using hind legs has never been observed. These facts suggest that the sexually dimorphic hind legs of this species can be explained by intersexual selection or sexual conflict. More interestingly, the male hind femur is thicker in populations at more southern latitudes, suggesting that the evolution of the sexual trait is constrained or modified by environmental factors that vary with latitude (Satomi et al. 2019).

In this study, we characterized morphological variation in sexually dimorphic traits within and between populations of the false blister beetle *O. sexualis*. We first quantified sexual dimorphism and differentiation among three populations in male and female body size, hind leg size, and hind femur shape. Then, we assessed scaling relationships between hind leg femur width and body size in both sexes in each population to detect constraints. Based on the results, we discuss the evolutionary forces and constraints that result in the differentiation in sexually selected traits.

MATERIALS AND METHODS

Organism and sampling

Oedemera sexualis is endemic to the Japanese Archipelago and is distributed from the southern end of the Ryukyu Islands to the western part of Honshu mainland (Svihla 1999). Adults aggregate on flowers (e.g., *Castanopsis sieboldii* and *Melia azedarach*) in coastal areas from the end of March to June. The active season of a single population is restricted to about 1–2 months and varies along latitudes.

We collected 581 wild individuals from three localities (Amami Oshima, 28°27'N, 129°36'E, 106 males and 99 females; Naruto, 34°12'N, 134°36'E, 106 males and 102 females; Yonaguni-jima, 24°27'N, 122°58'E, 88 males and 80 females) in Japan from 2002 to 2012 (hereafter Amami, Naruto, and Yonaguni, respectively) (Fig. S1). Live beetles were transferred to the laboratory and then frozen at -20°C. These three populations were representative of the 22 populations examined by Satomi et al. (2019). The Naruto and Yonaguni populations are situated near the northeastern-most and southwestern-most regions within the range of the species, respectively. The Amami population is situated at an intermediate latitude but has an exceptionally narrow male hind femur (Satomi et al. 2019), and male mating behavior differs from that in other populations (Koshio et al., unpublished data). Although south-western populations distributed in the Ryukyu Archipelago (including Amami and Yonaguni populations) are recognized as a different subspecies from populations in the northern mainland based on genital features (Svihla 1999), morphological variation in the hind legs does not support this classification.

Variation in body and hind leg sizes

To quantify phenotypic differences between the sexes and within and between populations, four dimensions of male and female hind legs were measured: hind femur length (FL), hind femur width (FW), hind tibia length (TL), and hind tibia width (TW). First, hind legs were removed from the body, and the femurs and tibiae were separated from each other. Then, these parts were stuck on drafting paper and the four characters (FL, FW, TL, and TW) were measured using a digital sight imaging controller (Nikon

DS-L2; Nikon, Tokyo, Japan) integrated into a binocular microscope to the nearest 0.01 mm (Fig. 1d). Elytron length (EL) was also measured as a proxy of body size. Traits were measured bilaterally, and two measurements of the left and right parts were averaged prior to subsequent analyses. These measurements are highly repeatable (Satomi et al. 2019).

To examine differences in body size (EL) and hind leg sizes (FL, FW, TL, and TW) between the sexes and among populations, generalized linear models (GLMs) were constructed with a normal distribution and identity link function, treating one of the traits as the objective variable and population, sex, and their interaction as explanatory variables.

Variation in male hind femur shape

For comparisons of the shape of male hind femurs, the most prominent sexual trait in *O. sexualis*, an elliptical Fourier (EF) analysis, was used (Kuhl and Giardina 1982). Images of hind femurs were obtained using a CCD camera attached to a binocular microscope (Nikon DS-L2), as described above, for a subset of samples (Amami: 13 males; Naruto: 10; Yonaguni: 15). Various programs implemented in the SHAPE package (Iwata and Ukai 2002) were used for subsequent analyses. Prior to the calculation of EF scores, we implemented noise reduction and binarization of the images and finally obtained contour information as chain codes using ChainCoder. Based on the chain codes, EF coefficients were estimated for each contour using Chc2Nef. EF coefficients were normalized based on the first harmonic ellipse derived from the approximation of contours by Fourier series expansion (Kido 2015). The number of harmonics of EF coefficients was set at 30 (the default is 20), resulting in 87 non-trivial normalized coefficients for each specimen (the first three coefficients were nearly constant after normalization). The normalized EF coefficients for the specimens were then summarized by a principal component (PC) analysis implemented in PrinComp. To visualize shape variation, we reconstructed the contours of the average shape of femurs as well as those plus or minus two standard deviations (SD) derived from the square root of the eigenvalue of each PC (Rohlf and Archie 1984, Furuta et al. 1995). The contour reconstructions were generated using PrinPrint. Kruskal–Wallis (K–W) tests were performed to examine whether median shape features represented by each PC varied among populations. Dunn's (1964) post hoc test was adopted when a significant difference was detected by the K–W test.

Scaling relationships in hind femur width

Scaling relationships are often evaluated with log-transformed data to enable easier fitting using linear regression. However, several recent publications have suggested that log-transformation distorts the relationship between the predictor and response variables, and that modern non-linear regression techniques make log-transformation no longer necessary (Packard 2009, 2011, 2012, but see Kerkhoff and Enquist 2009). In addition, the use of raw data in comparisons of simple allometric and logistic models may be suitable for examining whether an arithmetic or geometric growth curve is more appropriate (see below for details). Accordingly, hereafter, raw data were used for the analysis.

To evaluate the degree of constraint on trait growth, simple allometric and logistic models were fitted to raw values of hind leg FW on body size (EL) and were compared based on goodness-of-fit. The simple allometric model is $\mathrm{FW} = a\mathrm{EL}^{b}$, equivalent to a simple linear regression of log-transformed values and is used to describe allometric relationships between trait and body sizes, assuming that trait size increases with increasing body size with a constant growth rate b. A logistic model may be preferred when the growth of a trait is accelerated at small body sizes, as in the simple allometric model, but is decelerated at large body sizes, indicative of constrained growth, resulting in sigmoidal curves, given by the following formula, for example:

$\mathrm{FW} = c/\{1 + d\exp(-e\mathrm{EL})\}$,

where c describes the range of FW, d represents the elevation of the curve, and e denotes the slope (Fig. S2). A constraint against the exaggeration of FW is inferred in a population with a smaller c but constant e compared with those of other populations. Three parameters were examined to test the difference among populations based on 95% confidence intervals. Model fitting was performed by the function *nls* in R version 3.2.3, and exponential and logistic models were compared using Akaike's information criteria (AIC) to select the best-fit model.

RESULTS

Variation in body and hind leg sizes

The degree of sexual dimorphism in body and hind leg sizes, except for TL, differed significantly among the three populations, as indicated by significant interactions between population and sex (Table 1).

Variation in male hind femur shape

In a principal component analysis based on normalized EF coefficients, the first three PCs accounted for 92.56% of the total variance in the shape features of male hind femurs (PC1, 82.98%; PC2, 5.61%; and PC3, 3.97%; Fig. 2). According to the reconstructed outlines along the PC axes, femurs were narrower to the left and wider to the right along PC1. The K–W test showed that median shape features represented by

PC1 varied significantly among populations ($\chi^2 = 31.43$, $P < 0.001$), although those represented by PC2 did not differ ($\chi^2 = 1.13$, $P = 0.568$). A post hoc test indicated significant differences in median shapes along PC1 between all pairwise combinations of populations (Naruto vs. Amami, $P = 0.005$; Yonaguni vs. Amami, $P < 0.001$; Naruto vs. Yonaguni, $P = 0.006$), suggesting that each population possesses distinctive shape features represented by PC1. PC2 represented variation in the distal end of femurs; however, this characteristic varied markedly within populations, and the ranges of scores overlapped. Although PC3 accounted for only 3.97% of the total variance, a significant difference in median shapes was detected between the Naruto and Yonaguni populations (Dunn's test: $P < 0.001$). On average, the proximal end of femurs tended to be wider in Naruto and narrower in Yonaguni.

Scaling relationships in hind leg femur width

Based on simple allometric models, male FW showed significant positive allometry (Amami: $b = 1.28$ [95% confidence interval, 1.16–1.41]; Naruto: 1.29 [1.18–1.40]; Yonaguni: 1.28 [1.17–1.39]), while female FW was isometric (Amami: 0.94 [0.83–1.05]; Naruto: 1.07 [0.95–1.19]; Yonaguni: 1.07 [0.96–1.18]). These slopes did not differ among populations based on 95% confidence intervals.

The scaling relationships between male FW and EL were best described by logistic models in all three populations. ΔAIC values for the second-best simple allometric models were >2 in the Amami and Naruto populations (Fig. 3, Table 2), indicating that logistic models outperformed simple allometric models. However, the ΔAIC value for the Yonaguni population was 0.83, indicating that the two models performed similarly. The scaling relationships between female FW and EL were best described by simple allometric models in all three populations. However, ΔAIC values for the second-best logistic models were consistently <2 across populations (Fig. 3, Table 2), indicating a similar performance. Curves fitted to male FW did not overlap among populations, indicating that the difference in male FW among populations was not a byproduct of a body size difference, while curves fitted to female FW mostly overlapped among populations (Fig. 3). Variation in male FW within populations was smallest in Amami, followed by Naruto and Yonaguni, corresponding with the comparison of population means for male FW (Table 1, Fig. 3). Variation in male FW within each population was unimodal (Fig. 3).

The range of male FW was smallest in Amami and largest in Yonaguni, as indicated by the parameter *c*, while the slope *e* was constant across populations (Table 3). With respect to the parameter *c*, we found that (1) estimates differed significantly between Amami and other populations, and (2) estimates differed significantly between the Naruto and Yonaguni population in one direction of the comparison (i.e., *c* in Yonaguni fell outside of the 95% confidence interval of *c* in Naruto) (Table 3). By contrast, there was no significant difference in the estimates of *d* and *e* among populations (Table 3), and these estimates did not correspond with the population means of male FW (Table 1). Note that broad confidence intervals were obtained for *d*, indicating uncertainty. This may be explained by our data consisting of only the upper half of the sigmoidal curve (Figs. 3 and S2), which are insufficient to estimate this parameter.

DISCUSSION

Differentiation in sexual traits among populations is one of the major predictions of the theories of sexual selection and sexual conflict (Andersson 1982, Gavrilets 2000). In this study, we quantified sexual dimorphism in hind leg sizes and variation among populations in the false blister beetle *O. sexualis*, characterized by particularly developed male hind femurs. In accordance with analyses of geographical variation in external morphology (Satomi et al. 2019), we found that both male and female hind leg sizes and the degree of sexual dimorphism differ significantly among populations. EF analysis also revealed that inter-population variation in male hind femur shape can be largely attributed to variation in width as captured by PC1 and is slightly related to variation in the shape of the proximal end of hind femur as captured by PC3.

Our analyses of scaling relationships between hind FW and body size revealed that the growth rates of the trait were constant across populations in males and females based on the growth rate parameters (*b* in simple allometric models and the parameter *e* in logistic models), indicating that the pattern of relative investment in the trait was similar among populations. Constrained growth at large trait sizes as suggested by logistic models might influence the interpretation of slopes in simple allometric models; however, the observed curvilinearity was not strong (Fig. 3). Constant positive allometric slopes in male FW and constant isometric slopes in female FW suggest that selective regimes for the hind femur are similar among populations but different between the sexes. This may explain the sexual dimorphism in the hind femur in this species. However, the observed variation in the degree of sexual dimorphism among populations (Table 1) requires an additional explanation.

Our analyses of scaling relationships revealed that limits to the exaggeration of the male hind femur may differ among populations. Logistic models were preferred in two populations with relatively less exaggerated male hind femurs (Amami and Naruto), while the simple allometric model and logistic model fit equally well in the population with the most exaggerated male hind femur (Yonaguni). This suggests that the growth of male FW is virtually unconstrained at large trait sizes in the Yonaguni population. The estimates of c in the logistic models suggest that the range of male FW is smallest in Amami and largest in Yonaguni (Table 3), consistent with results for population means of male FW (Table 1, Fig. 3). Thus, observed variation in the male sexual trait among populations can likely be explained by variation in the limit to the exaggeration of the trait (Table 3). Since the estimation of the parameter d in logistic models involved substantial uncertainty, it was difficult to determine whether basal investment in the sexual trait was constant across populations.

The observed relationships between the inferred degrees of constraint on trait exaggeration and mean trait values among populations are not consistent with the predictions of the hypothesis that resource competition between body parts constrains the exaggeration of sexual traits (i.e., trait growth is more strongly constrained in species or populations with relatively large traits) (Knell et al. 2004, Tomkins et al. 2005). Conversely, our findings suggest that stronger limits to exaggeration decreased mean male sexual trait sizes. In addition, the distribution of male FW was not bimodal, suggesting that the observed nonlinear allometry is not associated with alternative mating tactics occasionally found in weaponry traits (e.g., Moczek and Emlen 2000). Indeed, alternative mating strategies have not been observed in *O. sexualis* males (Koshio et al., unpublished data).

Theory predicts that differentiation in a sexual trait can result from variation in the balance between sexual and natural selection, in which trait elaboration by sexual selection is limited by the costs of bearing the elaborated trait (Svensson and Gosden 2007). Thus, constraints on the growth of elaborated sexual traits may depend on the ecological context. For example, males with disproportionately large sexual traits may experience increased predation due to conspicuousness (Remmel and Tammaru 2009). Such natural selection may be particularly strong in populations experiencing intensive predation. However, the influence of exaggerated male hind femur on flight ability and geographical variation in predator abundance remain to be investigated in *O. sexualis*. Given the latitudinal cline of male sexual traits in this species (Satomi et al. 2019) and the stronger constraint detected in the northernmost population (Naruto) than in the southernmost population (Yonaguni), environmental factors driving natural selection against sexual trait growth may also contribute to latitudinal variation. Although the Amami population is found at an intermediate latitude within the range of the species (Fig. S1), it shows an exceptionally narrow male hind FW and constitutes an outlier along the latitudinal cline (Satomi et al. 2019), implying that environmental factors independent of latitude influence the trait in the Amami population. Alternatively, male mating behavior and traits responsible for mating success are distinct in this population (Koshio et al., unpublished data), suggesting that sexual selection shifted male femur shapes toward different optima from those of other populations. Note that male body size in the Amami population is relatively small (Fig. 3). However, any change in the sexual selection regime in the Amami population has not altered the growth rate of the trait, as revealed by our analyses.

In conclusion, we characterized variation in sexually dimorphic hind femurs in three selected *O. sexualis* populations. Scaling relationships in male femur width were best explained by logistic models, and the degree of constraint on large traits varied among populations. Contrary to the expectation from resource competition among body parts, limits to trait exaggeration were stronger in populations with smaller trait sizes. Natural selection (e.g., due to predation) might explain the observed patterns in trait variation. The results of this study provide insight into environment-dependent sexual trait evolution and diversification.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Figure S1. Locations of three sample populations of *O. sexualis* (Yonaguni, Amami, and Naruto). Shading indicates the species distributional range.

Figure S2. Effects of parameter changes in the logistic curve: (a) the parameter *c* determining the range of the curve; (b) the parameter *d* determining the elevation of the curve; and (c) the parameter *e* determining the slope of the curve. Bold curves fit the Amami male data (points shown), and simple and dashed curves indicate ±10% and ±20% of parameter values, respectively. Note that a larger *d* -value results in a lower curve.

Figure legends

Figure 1 Sexual dimorphism of hind legs and mating behavior in *O. sexualis* in the Naruto population: (a) male, (b) female, (c) male struggling to copulate with a female, and (d) measurements of five morphological traits. Scale bar = 5 mm for (a) and (b).

Figure 2 Difference in male hind femur shape among three populations of *O. sexualis* as revealed by an elliptical Fourier analysis: (a) PC1 vs. PC2 and (b) PC1 vs. PC3.

Figure 3 Scaling relationships between body size and male (circles) and female (crosses) hind femur widths in *O. sexualis*. The best-fit logistic and simple allometric curves for males and females, respectively, are shown for the (a) Amami population, (b) Naruto population, and (c) Yonaguni population. Grey points indicate the full range of variation by combining all populations. Histograms indicate variation in male femur widths.

Table 1 Generalized linear models (GLMs) explaining phenotypic variation in elytron length (EL) and four hind leg measurements (FL, FW, TL, and TW) in *Oedemera sexualis*. Means ± SD (mm) are shown.

	Amami		Naruto		Yonaguni		GLM		
Trait	Male	Female	Male	Female	Male	Female	Population	Sex	Population × sex
EL	5.546 ± 0.480	6.099 ± 0.622	6.121 ± 0.616	6.269 ± 0.654	5.872 ± 0.566	6.003 ± 0.621	$F_{2,575} = 22.28$***	$F_{1,575} = 32.84$***	$F_{2,575} = 8.05$***
FL	1.882 ± 0.167	1.917 ± 0.218	2.015 ± 0.193	1.925 ± 0.216	2.062 ± 0.180	1.943 ± 0.222	$F_{2,575} = 14.29$***	$F_{1,575} = 10.85$**	$F_{2,575} = 8.22$***
FW	0.588 ± 0.073	0.360 ± 0.039	0.883 ± 0.125	0.369 ± 0.047	1.014 ± 0.134	0.371 ± 0.046	$F_{2,575} = 348.88$***	$F_{1,575} = 3940.92$***	$F_{2,575} = 287.35$***
TL	1.846 ± 0.161	2.260 ± 0.254	1.977 ± 0.202	2.306 ± 0.263	1.871 ± 0.182	2.260 ± 0.266	$F_{2,575} = 10.52$***	$F_{1,575} = 416.06$***	$F_{2,575} = 2.01^{\mathrm{NS}}$
TW	0.235 ± 0.035	0.195 ± 0.023	0.304 ± 0.048	0.208 ± 0.027	0.329 ± 0.059	0.185 ± 0.026	$F_{2,575} = 82.24$***	$F_{1,575} = 796.20$***	$F_{2,575} = 84.71$***

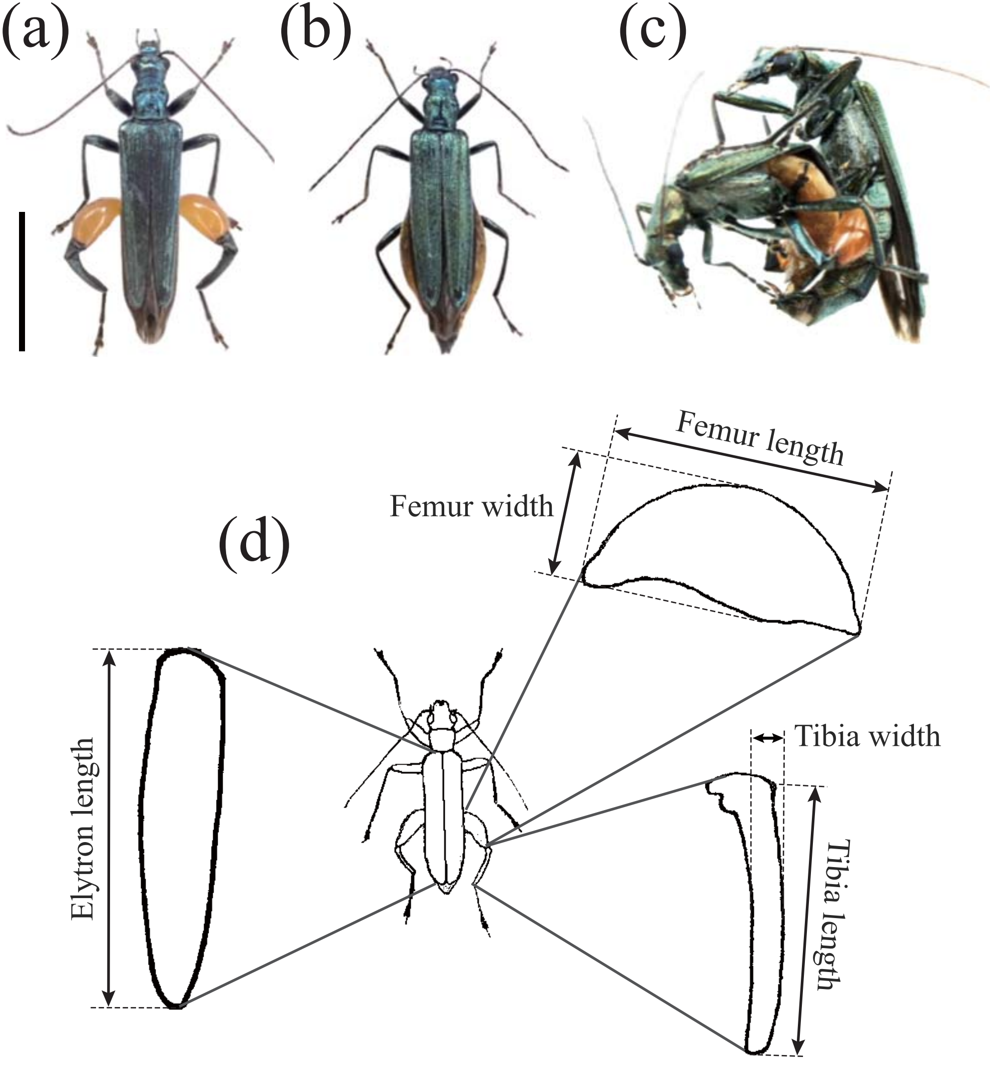
$^{\mathrm{NS}}P > 0.05$, **$P < 0.01$, ***$P < 0.001$. FL, femur length; FW, femur width; TL, tibia length; TW, tibia width.

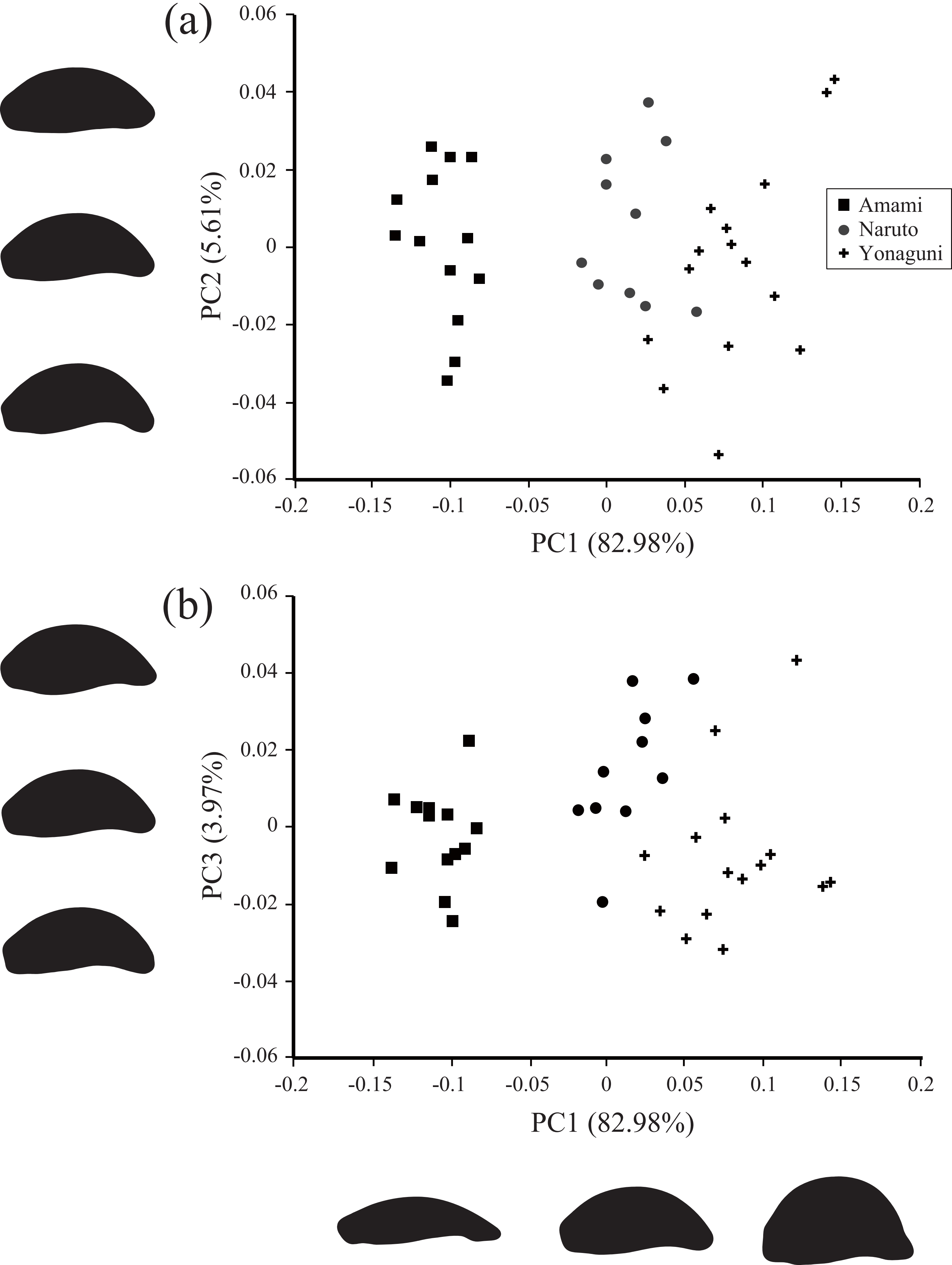
Table 2 Best-fit models for the scaling relationships between hind femur width and elytron length in three populations of *O. sexualis*

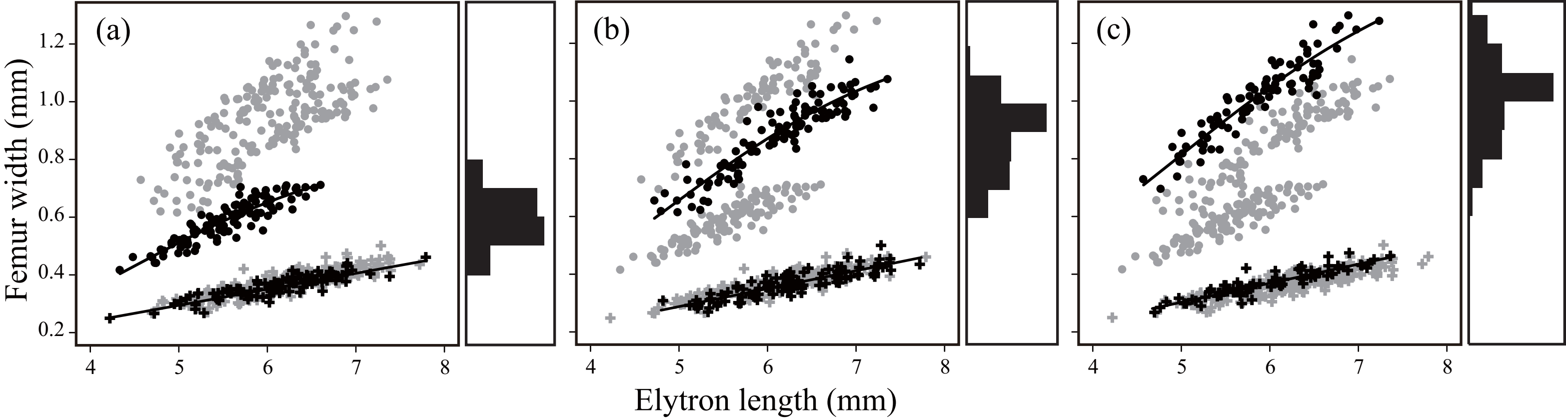
Trait	Model	Amami		Naruto		Yonaguni	
		AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
Male FW	Logistic	-425.29	0	-341.82	0	-279.58	0
	Simple	-422.69	2.6	-335.59	6.23	-278.75	0.83
Female FW	Logistic	-498.74	1.94	-473.48	1.23	-400.69	1.57
	Simple	-500.68	0	-474.71	0	-402.26	0

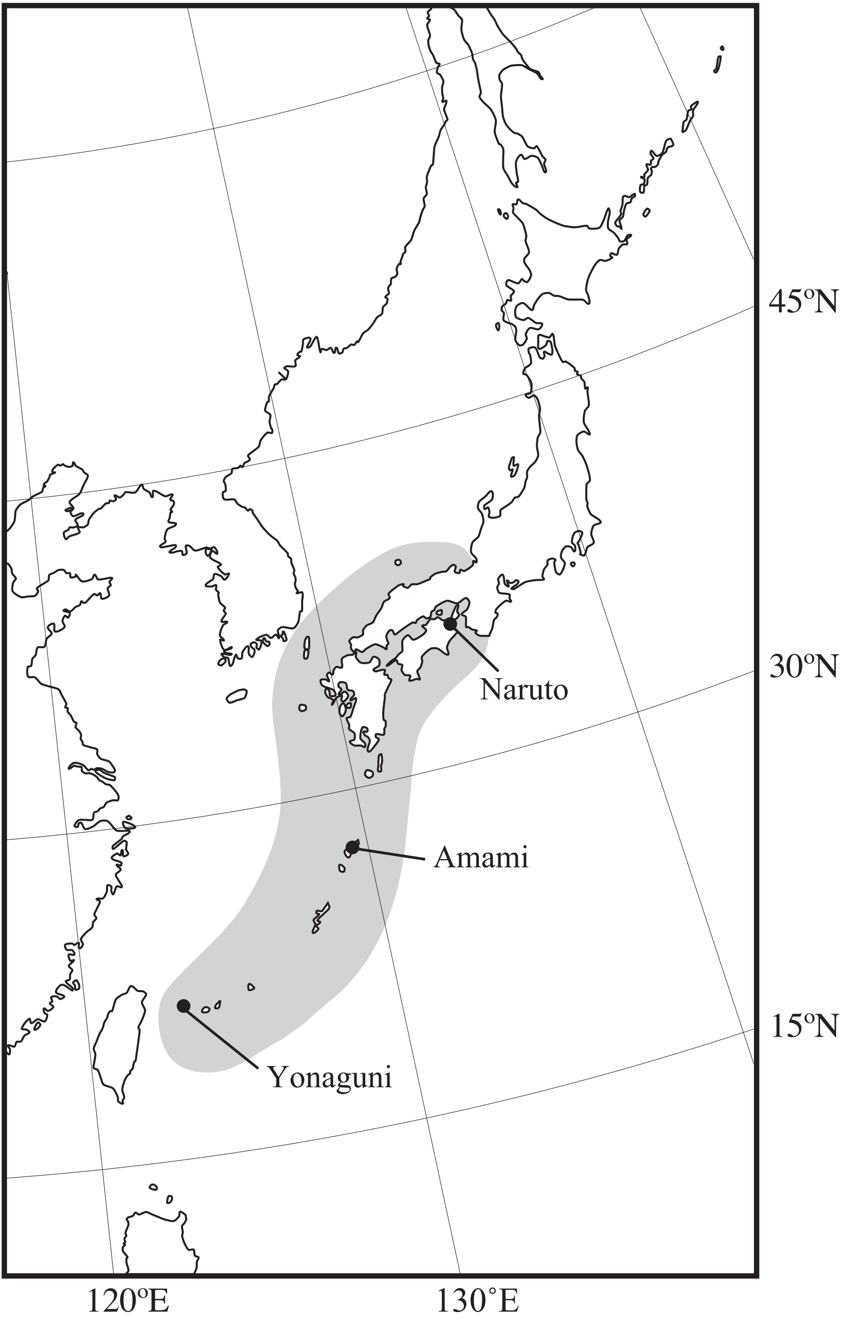
Table 3 Coefficients and 95% confidence intervals (CI) for logistic models describing scaling relationships between male FW and EL

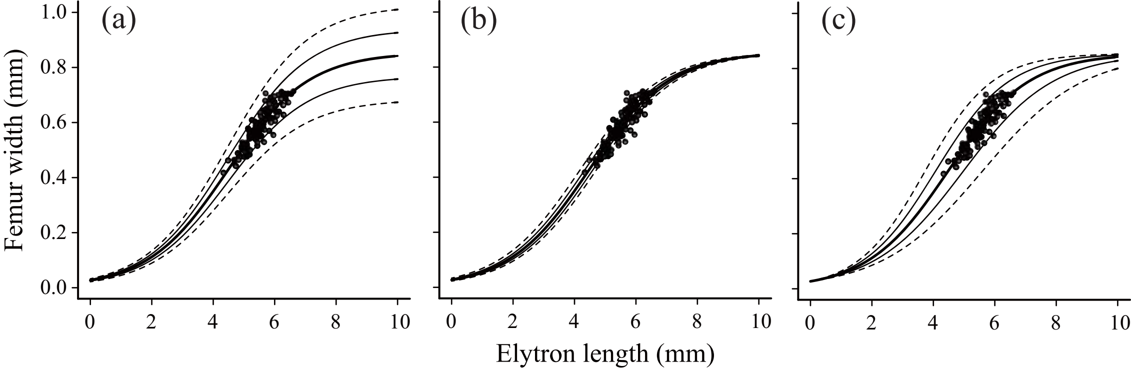
Population	*c*	95% CI	*d*	95% CI	*e*	95% CI
Amami	0.854	0.687–1.021	30.609	-7.021–68.239	0.764	0.427–1.101
Naruto	1.261	1.073–1.449	33.234	-0.223–66.691	0.717	0.466–0.968
Yonaguni	1.587	1.220–1.954	20.741	2.613–38.869	0.616	0.357–0.875


(a)
(b)
(c)
(d)
Femur length
Femur width
Tibia width
Elytron length
Tibia length


(a)
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
PC2 (5.61%)
-0.2
-0.15
-0.1
-0.05
0
0.05
0.1
0.15
0.2
PC1 (82.98%)
■ Amami
● Naruto
✚ Yonaguni
(b)
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
PC3 (3.97%)
-0.2
-0.15
-0.1
-0.05
0
0.05
0.1
0.15
0.2
PC1 (82.98%)


(a)
(b)
(c)
Femur width (mm)
1.2
1.0
0.8
0.6
0.4
0.2
4
5
6
7
8
Elytron length (mm)


45ºN
30ºN
15ºN
120ºE
130˚E
Naruto
Amami
Yonaguni


(a)
(b)
(c)
Femur width (mm)
0.0
0.2
0.4
0.6
0.8
1.0
0
2
4
6
8
10
Elytron length (mm)