Journal of Asia-Pacific Entomology 21 (2018) 1233–1238

Contents lists available at ScienceDirect

Journal of Asia-Pacific Entomology

journal homepage: www.elsevier.com/locate/jape

Full length article

Captive breeding of two insular populations of *Pachyrhynchus sarcitis* (Coleoptera: Curculionidae) from Lanyu and Babuyan Islands

Lung-Chun Huang[a], Wen-San Huang[b], Chung-Ping Lin[c], Olga M. Nuñeza[d], Hui-Yun Tseng[b,*], Hsin-Chieh Tang[a,*]

[a] *Conservation and Research Center, Taipei Zoo, No. 30, Sec. 2, Xinguang Rd., Taipei, Taiwan*
[b] *Department of Zoology, National Museum of Natural Science, No. 1,Kuan-Chien Rd., Taichung, Taiwan*
[c] *Department of Life Science, National Taiwan Normal University, No. 88, Sec. 4, Tingzhou Rd., Taipei, Taiwan*
[d] *Department of Biological Sciences, Mindanao State University–Iligan Institute of Technology, Tibanga, Iligan City, Philippines*

ARTICLE INFO

Keywords:
Conservation
Endangered species
Island endemics
Life history
Taiwan
The Philippines

ABSTRACT

Endemic species of oceanic islands are vulnerable due to their geographical isolation and small population sizes. For endangered island species, captive breeding program is an important strategy for conservation and sustainable management. *Pachyrhynchus sarcitis* is a flightless weevil decorated with colourful markings and distributed exclusively on several islets of Southeast Asia including Lanyu, Ludao, and Babuyan Islands. The life history of threatened *Pachyrhynchus* species of these islands was poorly known. This study reared *P. sarcitis* from Lanyu and Babuyan Islands for the first time in the laboratory using their host plant (*Leea guineensis*). The two island populations showed significant differences in instar numbers, in which the weevils from Lanyu Island had a higher instar number regardless the length of developmental duration. The adult body size of both sexes of the Babuyan population became smaller under laboratory condition; whereas Lanyu population in the laboratory did not show this trend. The differences in larval development might suggest local adaptation to the host plants or other life history associated characteristics which requires further research.

Introduction

Endemic species of oceanic islands are vulnerable due to geographic isolation, small population size and habitat destruction (Losos and Ricklefs, 2009). Therefore, island species may face higher risk of extinction than their mainland counterparts (Frankham, 1998; Kier et al., 2009). *Pachyrhynchus* weevils (Coleoptera: Curculionidae) are a group of insects decorated with astonishing colouration. They distributed on the Southeast Asian islands from the southern Ryukyus to New Guinea, and 90% of the species were endemic in the Philippines (Schultze, 1923). These weevils are flightless due to the fused elytra which may have limited their dispersal to the remote oceanic islands of Southeast Asia (Schultze, 1923). Although these colourful *Pachyrhynchus* weevils are popular among amateur collectors and researchers, current knowledge of their life history is poorly known, with only a limited number of studies on the mechanism of structural colours (Seago et al., 2009; Welch et al., 2007), biological function of colouration (Tseng et al., 2014), host plants (Hsu et al., 2017; Kayashima, 1940; Oshiro, 1991), secondary defense mechanism (Wang et al., 2018), taxonomy (Barševskis, 2016; Bollino and Sandel, 2015; Chen et al., 2017; Rukmane and Barševskis, 2016; Yoshitake, 2012) and biogeography (Tseng et al., 2018). The detailed information of larval development of *Pachyrhynchus* weevils is still lacking perhaps due to the difficulty of rearing them in the laboratory and the difficulty of finding larvae and eggs in the field (Hsu et al., 2017).

Pachyrhynchus sarcitis sarcitis (Behrens, 1887) was originally described from Calayan Island, which is one of the Babuyan Islands north of Luzon, the Philippines (Behrens, 1887; Schultze, 1923). This species is characterized for its glossy black body covered with pale green or pale flesh-coloured spots. In 1930, a population of this species having a black body decorated with green and blue spots, was described as a subspecies *P. sarcitis kotoensis* (Kôno, 1930) from Lanyu (Kôtôshô) (Kôno, 1930) and Ludao (Green Island; (Starr and Wang, 1992)) off shore from southeast Taiwan (Fig. 1A). Although only two subspecies have been described from the three islands (*P. s. sarcitis* on Calayan, *P. s. kotoensis* on Lanyu and Ludao), a different *P. sarcitis* population was discovered from Babuyan Island during our expedition to Babuyan Islands. This *P. sarcitis* population has distinct glossy dark purplish colouration decorated with pale yellow spots (Fig. 1B). In geological history of islands, Lanyu, Ludao and Babuyan Islands are all belonged to

* Corresponding authors.
E-mail addresses: hytseng@mail.nmns.edu.tw (H.-Y. Tseng), tgx02@zoo.gov.tw (H.-C. Tang).

https://doi.org/10.1016/j.aspen.2018.09.004
Received 25 June 2018; Received in revised form 13 August 2018; Accepted 10 September 2018
Available online 12 September 2018
1226-8615/

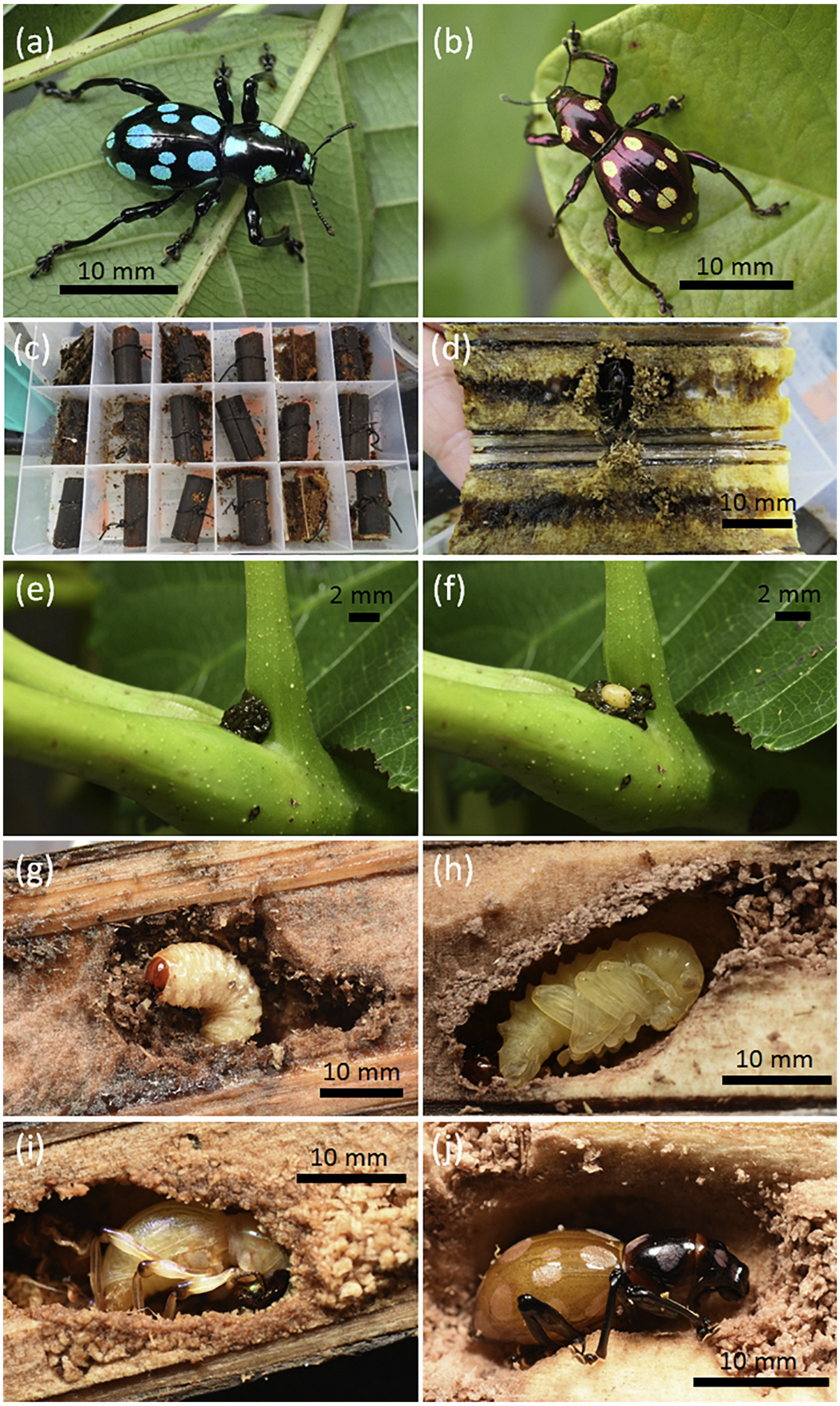

Fig. 1. Life stages of *Pachyrhynchus sarcitis*. (A) Adult of *Pachyrhynchus sarcitis kotoensis* from Lanyu, Taiwan; (B) adult of *Pachyrhynchus sarcitis* from Babuyan Island, the Philippines; (C, D) larvae were fed on the stems of *Leea guineensis* under laboratory conditions; (E) eggs of *Pachyrhynchus sarcitis kotoensis* from Lanyu were covered by feces; (F) feces were removed from the egg of *Pachyrhynchus sarcitis kotoensis*; (G) larva of *Pachyrhynchus sarcitis kotoensis* from Lanyu Island; (H) pupa of *Pachyrhynchus sarcitis kotoensis* from Lanyu Island in the pupal chamber; (I, J) newly emerged adults of *Pachyrhynchus sarcitis kotoensis* in pupal chamber showing the faint colour spots. I and J are different individuals. The black bars represent the scales.

Taiwan-Luzon volcanic Arc. This volcanic arc is generated by the subduction of the South China Sea which collided with the eastern margin of the Eurasian Plate. These three islands did not connect with other islands in the glacial period. Despite of the colour difference, a preliminary molecular phylogeny suggested close affinity among these populations (Tseng et al., unpublished data).

Captive breeding of endangered species is a useful and practical solution in conservation biology (Frankham, 2008; Griffiths and Pavajeau, 2008; Seddon et al., 2007). Captive breeding can help restore the population in the wild and obtain the life history information in the process. The populations of *P. sarcitis* endemic to Lanyu (47 km^2) and Ludao (16 km^2) Islands were listed as a “rare and valuable species” (Category II) by the Wildlife Conservation Act in Taiwan because of their small population sizes, heavy threats from tourism, collection pressure and habitat destruction (Chao et al., 2009). Under the serious threats of the ongoing habitat loss in these small islands, developing an effective rearing technique of *Pachyrhynchus* weevils in the laboratory is urgent and necessary for the conservation and research application.

Makihara (Makihara, 1975) and Starr and Wang (Starr and Wang, 1992) recorded a *Cissus* species (Vitaceae) and *Clematis gouriana* (Ranunculaceae) as the adult food plants of *P. s. kotoensis*, respectively. From our own field observations, many *P. s. kotoensis* adults fed on leaves of *Leea guineensis* (Leeaceae) and *L. philippinensis* on Lanyu Island, however, the host plant of *P. sarcitis* from Babuyan Islands was unknown. This study reported for the first time a new rearing procedure for *P. sarcitis* in the laboratory. Weevil populations from Lanyu and Babuyan Islands were reared on the host plant (*L. guineensis*), and the larval development and adult body sizes were recorded and compared.

Material and methods

Adults of *P. sarcitis* were collected from Babuyan (19°32′58″N, 121°54′40″E) and Lanyu (22°4′44.57″N, 121°33′15.25″E) Islands, respectively. Because most individuals were discovered on *L. guineensis* and *L. philippinensis*, the leaves of *L. guineensis* were used to feed adult weevils in the laboratory. Three individuals from Babuyan Island and eight from Lanyu Island were kept separately in plastic cages (34 × 25 × 22.5 cm) placed in a growth chamber with 12:12 h (L:D) photoperiod and 25 °C, 75% relative humidity (RH) in an insectarium of Taipei Zoo, Taiwan. Eggs of the weevils were checked every day.

To observe the developmental stages of the larvae, fresh stems of *L. guineensis* (ca. 3 cm in diameter and 5 cm in length) were split vertically into two parts (Fig. 1C, D). Each egg was buried into a stem, and checked for their larval stages every day by the presence of molted cuticles and the changes of their head width. When the stems were consumed completely by the larvae, we provided them with a fresh stem until the larvae molted into pupal stages. The duration of pupal stage were recorded once the adult emerged from the pupa. When the pupae emerged to adults, the weevils stayed in the chamber several days before leaving. The number of days from the emergence to the adult leaving the pupal chamber was recorded as the duration of imago stage. All larvae were kept in the same growth chamber and maintained at 25 °C and 75% relative humidity.

The length and width of the eggs, head width of the larvae, and adult body size were measured to the nearest 0.1 mm using a digital caliper (Mitutoyo, Kanagawa, Japan). Instar number and size difference between the two populations were compared using the Welch two sample *t*-test followed by a false discovery rate (FDR) correction and Fisher's exact test in R software (https://cran.r-project.org/), respectively. For the Lanyu population with a sufficient sample size (n = 70), Pearson's product-moment correlation coefficient in R was used to examine whether there is a correlation between the durations from egg to emergence and adult sizes. Welch two sample *t*-test was used to examine whether there is size difference between wild and captive breeding individuals in each population.

Results

Larval development

Under laboratory conditions, weevils laid eggs on the wall of cages or on the leaves of the plants. The eggs were usually covered with feces (Fig. 1E, F). Eggs from the Lanyu population were 2.31–2.93 mm (mean ± SE = 2.73 ± 0.13) in length and 1.60–1.97 mm (1.83 ± 0.07) in width. Eggs from the Babuyan population were 2.54–3.03 mm (2.82 ± 0.12) in length, 1.72–2.05 mm (1.86 ± 0.08) in width. The mean duration of egg stage was 20.79 ± 2.34 days (between 10 and 24) in the Lanyu and 20.68 ± 1.94 days (between 17 and 24) in the Babuyan population (Tables 1, 2).

The two populations showed significant difference in instar numbers (p = .038, Fisher's exact test). The Babuyan population had a lower number of instars from four (23%), five (68%), to six (9%). Although the majority of the Lanyu population had the same instars of four (5%), five (53%) and six (40%), they had a higher instar number and extended to seven (1%) and eight (1%) (Table 2; Fig. 2).

The first larval stage was 6–14 (9.55 ± 1.66) and 7–15 (9.32 ± 1.96) days in the Lanyu and Babuyan populations, respectively. In the second larval stage, larvae of Lanyu ranged from 9 to 28 days (15.02 ± 3.38), and larvae of Babuyan ranged from 12 to 20 days (15.45 ± 2.54). The durations of the third instar ranged from 13 to 29 (19.48 ± 3.16) and 15–33 days (22.59 ± 4.88) in the Lanyu and Babuyan populations, respectively. The difference of larval development had increased since the fourth (10–53 days, 24.73 ± 7.35), fifth (14–73 days, 35.72 ± 11.02) and sixth instar (13–63 days, 33.8 ± 11.60) of the Lanyu population, and the ranges of these instars were smaller (fourth instar: 15–46 days, 24.68 ± 7.87; fifth: 18–48 days, 34.65 ± 8.10; sixth: 39–43 days, 41.00 ± 2.83) in the Babuyan population.

For individuals with four instars, only the duration of the fourth instar was significantly different between two populations (50.26 ± 2.22 vs. 35.00 ± 8.34, $p < .05$), and the egg size and head width were similar (Table 1). There was no difference of the durations of the fifth instar between Lanyu and Babuyan individuals, but the head width of larvae from Lanyu in the fifth instar was significantly larger than that of larvae from Babuyan (2.95 ± 0.16 vs. 2.77 ± 0.15, $p < .05$). For the individuals with six instars, the duration of the third instar was longer (27 vs. 19.54 ± 3.67 days, $p < .05$), and the egg length (2.72 ± 0.13 vs. 2.89 ± 0.01, $p < .05$) and head width of the first instar larvae (1.14 ± 0.04 vs. 1.17 ± 0.01, $p < .05$) were larger in the Babuyan population, respectively. In the fifth instar, however, the larvae of Lanyu population became slightly larger than those of Babuyan population (2.80 ± 0.17 vs 2.73 ± 0.00, $p < .05$) (Table 1).

Adult body size

After emergence from pupal chamber, the blue or yellow colour markings started to appear during the first few minutes, and their bodies stayed soft until a few days later. Under laboratory conditions, the elytral length of adults in both sexes were significantly larger in Lanyu individuals (male: Lanyu, 9.80 ± 0.57 vs. Babuyan, 9.00 ± 0.50, $p < .05$; female: Lanyu, 10.51 ± 0.64 vs. Babuyan, 9.64 ± 0.57; $p < .05$), but the body width were similar in two populations (male: 6.25 ± 0.38 vs. 6.11 ± 0.41; female: 6.76 ± 0.46 vs. 6.84 ± 0.46). Compared to the wild populations, both captive breeding males and females became smaller in the Babuyan population (male: wild, n = 4, 10.48 ± 0.12 vs. CB, n = 15, 9.00 ± 0.50, $p < .05$; female: wild, n = 4, 11.17 ± 0.41 vs. CB, n = 14, 9.64 ± 0.57, $p < .05$), but not in the Lanyu population (male: wild, n = 8, 9.87 ± 0.67 vs. CB, n = 39, 9.80 ± 0.57; female: wild, n = 5, 10.68 ± 0.68 vs. CB, n = 31, 10.51 ± 0.64) (Fig. 3). In the Lanyu population, the duration between oviposition and adult emergence was from 123 to 227 days. Pearson's product-moment correlation coefficient (r) between the body sizes of males and females and the durations between eggs and adults was 0.04–0.25 (p = .80 and 0.18), respectively, suggesting that the male and female adult sizes had not increased when the growth duration increased.

Discussion

This study reported the first successful rearing for *Pachyrhynchus* weevils using their host plants. Compared to captive breeding of *P. infernalis*, of which larvae fed on sweet potatoes or artificial agar-based food (Anbutsu et al., 2017), *P. sarcitis* fed on *L. guineensis* showed a higher survival rate (ca. 80–90% vs. 13.7%). This might represent the suboptimal food for *P. infernalis* or different reproductive strategies (eggs of *P. sarcitis* are larger than that of *P. infernalis*, and larger eggs may have a higher survival rate). The rearing technique developed in this study not only facilitates future research projects, but also provides crucial information for the conservation of this endangered species with narrow geographical distribution. It could effectively reduce the

Table 1
Egg size and larval head width for each instar of *Pachyrhynchus sarcitis* from Lanyu and Babuyan Islands. Statistical significance was obtained from *t*-test with FDR correction between the two populations.

	4-instar individuals		*P*	5-instar individuals		*P*	6-instar individuals		*P*
	Lanyu (n = 4)	Babuyan (n = 5)		Lanyu (*n* = 46)	Babuyan (n = 15)		Lanyu (n = 35)	Babuyan (n = 2)	
Egg length	2.73 ± 0.08	2.77 ± 0.09	N.S.	2.74 ± 0.13	2.83 ± 0.14	N.S.	2.72 ± 0.13	2.89 ± 0.01	***
Egg width	1.85 ± 0.05	1.87 ± 0.07	N.S.	1.84 ± 0.07	1.86 ± 0.09	N.S.	1.82 ± 0.08	1.78 ± 0.03	N.S.
1st instar	1.14 ± 0.04	1.15 ± 0.02	N.S.	1.14 ± 0.04	1.12 ± 0.05	N.S.	1.14 ± 0.04	1.17 ± 0.01	*
2nd instar	1.56 ± 0.09	1.52 ± 0.06	N.S.	1.50 ± 0.07	1.49 ± 0.07	N.S.	1.51 ± 0.06	1.45 ± 0.12	N.S.
3rd instar	2.05 ± 0.08	2.03 ± 0.10	N.S.	1.95 ± 0.11	1.96 ± 0.13	N.S.	2.41 ± 2.96	1.91 ± 0.13	N.S.
4th instar	2.59 ± 0.11	2.48 ± 0.10	N.S.	2.43 ± 0.14	2.39 ± 0.11	N.S.	2.44 ± 0.55	2.30 ± 0.01	N.S.
5th instar				2.95 ± 0.16	2.77 ± 0.15	**	2.80 ± 0.17	2.73 ± 0.00	*
6th instar							3.27 ± 0.18	2.98 ± 0.14	N.S.

* $p < .05$.
** $p < .01$.
*** $p < .001$.

number of weevils needed from the wild population for research projects, and provides adequate number of individuals for releasing back to the islands after a careful assessment of conservation management programs.

Establishing an effective captive breeding technique is a critical first step in many research and conservation projects. One of the most famous examples is *Heliconus* butterfly (Mavárez et al., 2006; Melo et al., 2009). The speciation process and genetic control of wing colouration were revealed through captive breeding programs (Huber et al., 2015; Joron et al., 2006; Le Poul et al., 2014). *Pachyrhynchus* weevils display astonishing diversity of aposematic colouration and extremely high insular species diversity (Chen et al., 2017; Schultze, 1923; Tseng et al., 2014). Nevertheless, except for a few studies on the taxonomy and the structure and function of colours, relevant studies considering the ecology and evolution of their warning colouration, as well as the complex speciation histories on these islands, are largely unknown. It was until recent years that the aposematic function of colouration and the seconardy defense mechanism of *Pachyrhynchus* weevils were first verified in behavioral tests (Tseng et al., 2014; Wang et al., 2018). The ongoing research projects start to reveal the speciation mechanism, cryptic species and biogeographic histories of these weevils (Chen et al., 2017; Tseng et al., 2018). All these research systems require stable supplements of weevils with standardized genetic and environmental background, which made the captive breeding of these weevils became a critical technique.

The astonishing diversity of phytophagous weevils is often attributed to adaptation and co-evolution with angiosperms ((McKenna et al., 2009); Kitson et al., 2013), and the host plant plays an important role in

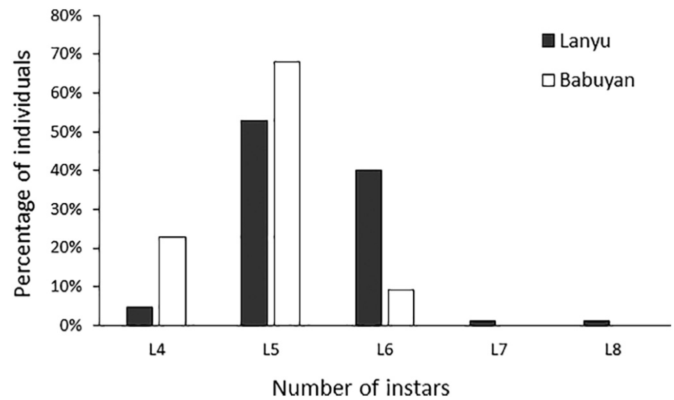

Fig. 2. Number of larval stages in *Pachyrhynchus sarcitis kotoensis* of Lanyu Island and *Pachyrhynchus sarcitis* from Babuyan Island.

the process of diversification in weevils (McKenna et al., 2009). Understanding the variation of larval development between island populations of *P. sarcitis* can facilitate initial recognition of potential host plant adaptation. Host shift to distantly related host plants during the process of inter-island diversification in *Pachyrhynchus* weevils may have provided the platform for speciation (Chen et al., 2017; Tseng et al., 2018). In this study, the adult body size of captive breeding individuals was similar to those of the wild population in Lanyu Island, but significantly smaller for the population from Babuyan Island. One probable explanation is the adaptation on local host plant species. On

Table 2
Duration (in days) of developmental stages of *Pachyrhynchus sarcitis* from Lanyu and Babuyan Islands. Statistical significance was obtained from *t*-test with FDR correction.

	4-instar individuals		*P*	5-instar individuals		*P*	6-instar individuals		*P*
	Lanyu (n = 4)	Babuyan (n = 5)		Lanyu (n = 46)	Babuyan (n = 15)		Lanyu (n = 35)	Babuyan (n = 2)	
Egg stage	22.3 ± 1.5	21.4 ± 1.1	N.S.	20.6 ± 2.3	20.3 ± 2.1	N.S.	20.8 ± 2.4	21.5 ± 2.1	N.S.
1st instar	8.8 ± 0.5	8.8 ± 1.3	N.S.	9.6 ± 1.8	9.5 ± 2.3	N.S.	9.5 ± 1.6	9.0 ± 0.0	N.S.
2nd instar	15.8 ± 4.7	17.2 ± 2.6	N.S.	14.7 ± 3.0	15.0 ± 2.5	N.S.	15.4 ± 3.7	14.5 ± 0.7	N.S.
3rd instar	22.5 ± 1.3	20.4 ± 3.3	N.S.	19.2 ± 2.7	22.7 ± 5.3	N.S.	19.5 ± 3.7	27.0 ± 0.0	***
4th instar	50.3 ± 2.2	35.0 ± 8.3	*	24.0 ± 5.1	22.2 ± 4.5	N.S.	22.7 ± 4.1	17.5 ± 3.5	N.S.
5th instar				39.6 ± 9.6	36.5 ± 6.5	N.S.	30.7 ± 10.8	20.5 ± 3.5	N.S.
6th instar							33.8 ± 11.6	41.0 ± 2.8	N.S.
Pupal stage	13.8 ± 2.1	14.8 ± 2.4	N.S.	16.0 ± 1.8	14.8 ± 1.5	N.S.	17.03 ± 1.0	17.0 ± 0.0	N.S.
Imago	6.0 ± 1.4	4.8 ± 2.2	N.S.	7.0 ± 1.9	6.7 ± 1.5	N.S.	6.5 ± 2.1	6.00 ± 0.0	N.S.
Total	133.3 ± 5.9	117.6 ± 6.9	N.S.	143.7 ± 10.3	141.1 ± 9.3	N.S.	169.5 ± 21.9	168.0 ± 7.1	N.S.

* $p < .05$.
*** $p < .001$.

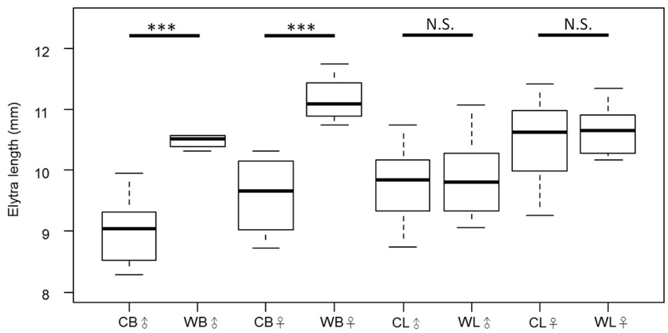

Fig. 3. Comparison of the body sizes between wild and captive breeding populations of *Pachyrhynchus sarcitis kotoensis* from Lanyu Island and *Pachyrhynchus sarcitis* from Babuyan Island. CB♂: captive Babuyan males; WB♂: wild Babuyan males; CB♀: captive Babuyan females; WB♀: wild Babuyan females; CL♂: captive Lanyu males; WL♂: wild Lanyu males; CL♀: captive Lanyu females; WL♀: wild Lanyu females. ***: $p < .001$, Welch two sample *t*-test.

Lanyu Island, *P. s. kotoensis* is usually found on *Leea* plants. However, the host plant of *P. sarcitis* was not recorded on Babuyan Island. Since the host plant of Babuyan *P. sarcitis* was not confirmed, the decreased larval performance and body size might due to the low food utilization, low nutrition conversion efficiency, or proteinase inefficiency (Messina, 2004; Milanović et al., 2016; Yang et al., 2008). The other potential factor that affect adult body size in Babuyan population might be environmental factors, such as ambient temperature which affects the duration and the growth rate of larva, and adult size in ectotherms (Angilletta Jr. et al., 2004; Antonatos et al., 2013; Ferro et al., 1985; Van der Have and De Jong, 1996). The environmental temperature in Lanyu (http://www.cwb.gov.tw/V7/climate/monthlyMean/Taiwan_tx.htm) is 2–4 °C lower than in Babuyan (https://www.yr.no/place/philippines/cagayan%20valley/babuyan%20island/statistics.html) during the whole year, and the smaller body size might due to the unsuitable temperature. Genetic effect of founder population may also be a possible reason that effect the body size of adult insects due to lower genetic diversity (Berggren, 2005), and in our case, only few individuals were included in the breeding experiment, which may cause the size differences between captive-breeding and wild populations.

The species number of *Pachyrhynchus* weevils remains under-estimated, where new *Pachyrhynchus* species are being described almost every year (Barševskis, 2016; Bollino and Sandel, 2015; Chen et al., 2017; Rukmane and Barševskis, 2016; Yoshitake, 2012). Several studies of *Pachyrhynchus* weevils suggested divergent or convergent evolution in their colouration and marking patterns (Rukmane, 2016; Schultze, 1923; Yoshitake, 2017), and the colourations of these weevils may have evolved rapidly (Tseng et al., 2018). Therefore, species delimitation of *Pachyrhynchus* weevils based only on colourations is difficult and insufficient (Chen et al., 2017). The two insular populations of *P. sarcitis* have different colours and adult sizes under a common laboratory condition, which may reflect the host adaptation, genealogy, and other life history associated characteristics. These results also suggest that they may represent two cryptic species, and further studies are needed to examine the species boundary of *P. sarcitis*.

Declarations of interest

None.

Acknowledgements

We are grateful to Hsin-Ping Ko for the suggestions of breeding technique, Shih-Jie Chiu, Chung-Yi Hsiao and Lu-Yi Wang for assistance of breeding weevils, Si-Min Lin for the helps in editing manuscript, Chen-Pan Liao for the assistance of statistics, and to the Council of Agriculture, Taiwan Executive Yuan of Taiwan for research and collecting permits (No. 1041700842). The Ministry of Science and Technology, Taiwan (MOST) of Taiwan provided financial support for this study (102-2621-B-178-001-MY3 & 105-2621-B-178-001 to W.-S. Huang and 103-2311-B-029-001-MY3 & 104-2621-B-003-002-MY3 to C.-P. Lin).

References

Anbutsu, H., Moriyama, M., Nikoh, N., Hosokawa, T., Futahashi, R., Tanahashi, M., Meng, X.-Y., Kuriwada, T., Mori, N., Oshima, K., 2017. Small genome symbiont underlies cuticle hardness in beetles. Proc. Natl. Acad. Sci. U. S. A. 114, E8382–E8391.
Angilletta Jr., M.J., Steury, T.D., Sears, M.W., 2004. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. Integra. Comp. Biol. 44, 498–509.
Antonatos, S.A., Emmanuel, N.G., Fantinou, A.A., 2013. Effect of temperature and species of plant on the consumption of leaves by three species of Orthoptera under laboratory conditions. Eur. J. Entomol. 110, 605–610.
Barševskis, A., 2016. New species of *Pachyrhynchus* Germar, 1824 and *Macrocyrtus* Heller, 1912 (Coleoptera: Curculionidae) from the Marinduque Island (Philippines) as a new example of mimetic species pair. Acta Biol. Univ. Daugavp. 16, 1–6.
Behrens, W., 1887. Materialien zu einer Monographie der Curculionengruppe Pachyrrhynchidae. Stett. Ent. Zeit. 48, 211–257 (In German).
Berggren, Å., 2005. Effect of propagule size and landscape structure on morphological differentiation and asymmetry in experimentally introduced Roesel's Bush-Crickets. Conserv. Biol. 19, 1095–1102.
Bollino, M., Sandel, F., 2015. Three new species of the genus *Pachyrhynchus* Germar, 1824 from Lubang Island (Philippines) (Curculionidae: Entiminae: Pachyrhynchini). Munis Entomol. Zool. 10, 392–401.
Chao, J., Yang, M., Wu, W., 2009. Setting Assessing Criteria for the Conservation of Taiwan's Threatened Insects. Council of Agriculture, Executive Yuan, Taiwan.
Chen, Y.-T., Tseng, H.-Y., Jeng, M.-L., Su, Y.-C., Huang, W.-S., Lin, C.-P., 2017. Integrated species delimitation and conservaiton implications of an endangered weevil *Pachyrhynchus sonani* (Coleoptera: Curculionidae) in Green and Orchid Islands of Taiwan. Syst. Entomol. 42, 796–813.
Ferro, D., Logan, J., Voss, R., Elkinton, J., 1985. Colorado potato beetle (Coleoptera: Chrysomelidae) temperature-dependent growth and feeding rates. Environ. Entomol. 14, 343–348.
Frankham, R., 1998. Inbreeding and extinction: island populations. Conserv. Biol. 12, 665–675.
Frankham, R., 2008. Genetic adaptation to captivity in species conservation programs. Mol. Ecol. 17, 325–333.
Griffiths, R.A., Pavajeau, L., 2008. Captive breeding, reintroduction, and the conservation of amphibians. Conserv. Biol. 22, 852–861.
Hsu, C.-F., Tseng, H.-Y., Hsiao, Y., Ko, C.-C., 2017. First record of the host plant and larvae of *Pachyrhynchus sonani* (Coleoptera: Curculionidae) on Lanyu Island, Taiwan. Entomol. Sci. 20, 288–291.
Huber, B., Whibley, A., Poul, Y., Navarro, N., Martin, A., Baxter, S., Shah, A., Gilles, B., Wirth, T., McMillan, W., 2015. Conservatism and novelty in the genetic architecture of adaptation in *Heliconius* butterflies. Heredity 114, 515–524.
Joron, M., Papa, R., Beltrán, M., Chamberlain, N., Mavárez, J., Baxter, S., Abanto, M., Bermingham, E., Humphray, S.J., Rogers, J., 2006. A conserved supergene locus controls colour pattern diversity in *Heliconius* butterflies. PLoS Biol. 4, 1831–1840.
Kayashima, I., 1940. Notes on a weevil (*Pachyrrhynchus moniliferus* Germ.) injurious to cacao fruit in the Philippine Islands. Trans. Nat. Hist. Soc. Formosa 30, 126–129.
Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J., Barthlott, W., 2009. A global assessment of endemism and species richness across island and mainland regions. Proc. Natl. Acad. Sci. U. S. A. 106, 9322–9327.
Kitson, J.J., Warren, B.H., Vincent, Florens F., Baider, C., Strasberg, D., Emerson, B.C., 2013. Molecular characterization of trophic ecology within an island radiation of insect herbivores (Curculionidae: Entiminae: Cratopus). Mol. Ecol. 22, 5441–5455.
Kôno, H., 1930. Kurzrüssler aus dem Japanischen Reich. J. Fac. Agric. Hokkaido Univ. 24, 153–242 (In German).
Le Poul, Y., Whibley, A., Chouteau, M., Prunier, F., Llaurens, V., Joron, M., 2014. Evolution of dominance mechanisms at a butterfly mimicry supergene. Nat. Commun. 5, 5644.
Losos, J.B., Ricklefs, R.E., 2009. Adaptation and diversification on islands. Nature 457, 830–836.
Makihara, H., 1975. A List of Coleoptera from Formosa by the Member of the Kagoshima University Biological Club. Formosan Expedition Kagoshima University Biological Club (Coleoptera), Kagoshima (In Japanese).
Mavárez, J., Salazar, C.A., Bermingham, E., Salcedo, C., Jiggins, C.D., Linares, M., 2006. Speciation by hybridization in *Heliconius* butterflies. Nature 441, 868–871.
McKenna, D.D., Sequeira, A.S., Marvaldi, A.E., Farrell, B.D., 2009. Temporal lags and overlap in the diversification of weevils and flowering plants. Proc. Natl. Acad. Sci. U. S. A. 106, 7083–7088.
Melo, M.C., Salazar, C., Jiggins, C.D., Linares, M., 2009. Assortative mating preferences among hybrids offers a route to hybrid speciation. Evolution 63, 1660–1665.
Messina, F.J., 2004. Predictable modification of body size and competitive ability following a host shift by a seed beetle. Evolution 58, 2788–2797.
Milanović, S., Janković-Tomanić, M., Kostić, I., Kostić, M., Morina, F., Živanović, B., Lazarević, J., 2016. Behavioural and physiological plasticity of gypsy moth larvae to host plant switching. Entomol. Exp. Appl. 158, 152–162.

Oshiro, Y., 1991. Studies on the *Pachyrhynchus infernalis* effecting *Mangifera indica* in Ishigaki Island. Okinawa Agric. 26, 19–23 (In Japanese).

Rukmane, A., 2016. Six new species of the genus *Pachyrhynchus* Germar, 1824 (Coleoptera: Curculionidae) from the Philippines. Acta Biol. Univ. Daugavp. 16, 77–89.

Rukmane, A., Barševskis, A., 2016. Nine new species of the genus *Pachyrhynchus* Germar, 1824 (Coleoptera: Curculionidae) from the Philippines. Balt. J. Coleopterol. 16, 77–96.

Schultze, W., 1923. A monograph of the pachyrrhynchid group of the Brachyderinae, Curculionidae: part 1. Philipp. J. Sci. 23, 609–673.

Seago, A., Brady, P., Vigneron, J., Schultz, T., 2009. Gold bugs and beyond: a review of iridescence and structural colour mechanisms in beetles (Coleoptera). J. R. Soc. Interface 6, S165–S184.

Seddon, P.J., Armstrong, D.P., Maloney, R.F., 2007. Developing the science of reintroduction biology. Conserv. Biol. 21, 303–312.

Starr, C.K., Wang, H.-Y., 1992. Pachyrhynchine weevils (Coleoptera: Curculionidae) of the islands fringing Taiwan. J. Taiwan Mus. 45, 5–14.

Tseng, H.-Y., Lin, C.-P., Hsu, J.-Y., Pike, D.A., Huang, W.-S., 2014. The functional significance of aposematic signals: geographic variation in the responses of widespread lizard predators to colourful invertebrate prey. PLoS One 9, e91777.

Tseng, H.-Y., Huang, W.-S., Jeng, M.-L., Villanueva, R.J.T., Nuñeza, O.M., Lin, C.-P., 2018. Complex inter-island colonization and peripatric founder speciatio promote diversification of flightless *Pachyrhynchus* weevils in the Taiwan-Luzon volcanic belt. J. Biogeogr. 45, 89–100.

Van der Have, T., De Jong, G., 1996. Adult size in ectotherms: temperature effects on growth and differentiation. J. Theor. Biol. 183, 329–340.

Wang, L.-Y., Huang, W.-S., Tang, H.-C., Huang, L.-C., Lin, C.-P., 2018. Too hard to swallow: a secret secondary defence of an aposematic insect. J. Exp. Biol. 221, jeb172486.

Welch, V., Lousse, V., Deparis, O., Parker, A., Vigneron, J.P., 2007. Orange reflection from a three-dimensional photonic crystal in the scales of the weevil *Pachyrrhynchus congestus pavonius* (Curculionidae). Phys. Rev. E 75, 041919.

Yang, S., Ruuhola, T., Haviola, S., Rantala, M.J., 2008. Effects of host-plant shift on immune and other key life-history traits of an eruptive Geometrid, *Epirrita autumnata* (Borkhausen). Ecol. Entomol. 33, 510–516.

Yoshitake, H., 2012. Nine new species of the genus *Pachyrhynchus* Germar (Coleoptera: Curculionidae) from the Philippines. Esakia 52, 17–34.

Yoshitake, H., 2017. Notes on Pachyrhynchini jewel weevils (Coleoptera: Curculinidae: Entiminae) and other insects showing remarkable resemblance in colour and body pattern characteristics. Gekkan-Mushi 22–40, 553 (In Japanese with English Abstract).