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Reproductive cycle and maturation of Swinhoe's tree lizard (*Diploderma swinhonis* (Günther, 1864)) in Hyuga City, Miyazaki Prefecture, Japan

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ABSTRACT. Swinhoe's tree lizard (*Diploderma swinhonis*) is an arboreal agamid that is native to Taiwan. The species has been introduced to some areas of Japan and is regarded as an invasive alien species. In 2016, a nonnative population of *D. swinhonis* was discovered in Hyuga City, Miyazaki Prefecture, Japan, but little information was available on the ecology of the population at the time. The main purpose of this study was therefore to investigate the reproductive cycle and maturation of this population. Field research was conducted from 2017 to 2019, and 764 lizards were collected. Euthanized lizards were dissected and the reproductive organs were examined to determine the reproductive period, clutch size, clutch frequency and size at sexual maturity. Females with oviductal eggs or vitellogenic ovarian follicles were observed from May to October. Clutch size ranged from 2 to 8, and clutch frequency was more than twice a year. In males, spermiogenesis started in early May and testicular regression was observed in September. Males with spermatozoa in the epididymides were found from May to November. Minimum snout-vent length at sexual maturity was 50.2 mm in females and 53.0 mm in males. Comparisons of the findings of this study and reports from Taiwan suggest that the nonnative population of *D. swinhonis* in Hyuga City has a higher fecundity than populations in Taiwan. It is therefore considered necessary to exterminate the population in Hyuga City before this species colonizes other areas.

KEY WORDS: clutch size, invasive alien species, reproductive period, spermiogenesis, Swinhoe's tree lizard

Although numerous species have been introduced into areas outside their natural range [11], many introduced species fail to become established and form viable populations [17]. However, if these species do become established, they can become invasive alien species, which are a significant threat to biodiversity and a major cause of native species extinction [2, 26].

Swinhoe's tree lizard (*Diploderma swinhonis* (Günther, 1864)) is an arboreal agamid that is found at elevations below 1,500 m on Taiwan and Orchid Island where it is native [24, 29]. *Diploderma swinhonis* (*D. swinhonis*) is diurnal, and males exhibit conspicuous territorial behavior that includes aggressive displays [9]. The species is an opportunistic sit-and-wait (ambush) predator that eats mainly ants, but also occasionally preys on insects as large as grasshoppers [22]. The habitat preference of *D. swinhonis* ranges from open forest to urban environments, such as school campuses [12]. Several authors have investigated the reproductive cycle and maturation of *D. swinhonis* in Taiwan [7, 15, 16, 23]. According to Huang [7], *D. swinhonis* is a seasonal breeder that is reproductively active from March to October. Females deposit 2 or 3 clutches of eggs a year, with clutch size ranging from 3.27 ± 0.16 (mean ± SD; range, 2–5) eggs [7].

In Japan, *D. swinhonis* has been introduced to several temperate areas —Iwata City in Shizuoka Prefecture, Atsugi City in Kanagawa Prefecture and Hyuga City in Miyazaki Prefecture—and is regarded as invasive alien species. Since 2016, the Japanese government has placed restrictions on raising, storing or transporting *D. swinhonis* through the provisions laid out in the Invasive Alien Species Act [20].

The population of *D. swinhonis* investigated in this study was discovered in Hyuga City in 2016. Hyuga City is located in the

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temperate zone of southeastern Kyushu Island. Since there is a difference in the climate of the temperate areas of Japan and the subtropical and tropical areas of Taiwan, the ecology of *D. swinhonis* in Hyuga City may differ from that in Taiwan. However, since there was little information about the ecology of this population in Hyuga City, this study compared the reproductive cycle and maturation of the *D. swinhonis* population in Hyuga City with populations in Taiwan.

MATERIALS AND METHODS

Animals

A total of 764 lizards were captured in Hyuga City, Miyazaki Prefecture, Japan (32°26′N, 131°39′E) from May 2017 to November 2019; no lizards were observed in the field from December to March. Upon returning to the laboratory, the lizards were euthanized by intracoelomic injection of sodium pentobarbital. Snout-vent length (SVL) and body weight (BW) were measured. All lizards were dissected and sexed based on their reproductive organs before being fixed in 20% buffered formalin. The study protocol was approved by the Institutional Animal Care and Use Committee of the University of Miyazaki, Japan (Approval No. 2018-016).

Observation of female reproductive organs

The gonads of 205 female lizards were subjected to morphological examination. Female reproductive status was determined based on the presence of vitellogenic ovarian follicles and oviductal eggs. Ovarian follicles greater than 3 mm in diameter were considered to be vitellogenic, as reported previously [7]. Females with vitellogenic ovarian follicles or oviductal eggs were considered to be reproductively active, and vitellogenic ovarian follicles and oviductal eggs were counted. The stage of the female reproductive cycle and clutch frequency were estimated based on the presence of oviductal eggs and vitellogenic ovarian follicles. The number of oviductal eggs or vitellogenic ovarian follicles was considered to reflect clutch size [7]. In cases where females possessed both oviductal eggs and vitellogenic ovarian follicles, clutch size was taken as the number of oviductal eggs. The smallest SVL of females with vitellogenic ovarian follicles or oviductal eggs was taken as the SVL at sexual maturity.

Observation of male reproductive organs

The gonads of 154 male lizards were subjected to histological examination. The testes and epididymides were removed, and measured the major axis, minor axis, and thickness using dial calipers. Testis size was estimated by multiply those three variables. The tissues were then fixed in 20% buffered formalin or 4% paraformaldehyde phosphate buffered saline before being embedded in paraffin and cut into 4 μm sections. The sections were then stained with hematoxylin and eosin and observed under a light microscope (Olympus Corporation, Tokyo, Japan). The presence of spermatozoa in seminiferous tubules and epididymal ducts was then examined. The male reproductive cycle was estimated based on seasonal changes observed in the spermatogenic epithelium. The smallest male with spermatozoa in the epididymal ducts was taken as the size at sexual maturity.

Statistical analysis

Student's *t*-test was used to compare the differences in SVL and BW between males and females. Pearson's regression analysis was used to clarify the relationship between female body size and clutch size, and between male body size and testis size. The Tukey-Kramer test was used to examine seasonal changes in testis size; to minimize the effect of body size, only large males (>70 mm SVL) were used for this analysis. A value of $P<0.05$ was considered significant and data was shown as means ± SD. Statistical analyses were performed using EZR (Saitama Medical Center, Jichi Medical University, Saitama, Japan), which is a graphical user interface for R (The R Foundation for Statistical Computing, Vienna, Austria) [10].

RESULTS

Morphology

Mature *D. swinhonis* individuals are sexually dimorphic for body size and color (Fig. 1), with mature males characterized by having a yellow line on their flanks (Fig. 1a). Mean SVL of immature lizards were 36.5 ± 9.1 mm (n=127; range, 20.5−52.3 mm). Mean BW of immature lizards was 1.8 ± 1.3 g (n=116; range, 0.12−4.81 g). Mean SVL of adult males was 72.6 ± 7.7 mm (n=396; range, 53.0−87.4 mm) and that of adult females was 62.1 ± 6.2 mm (n=183; range, 50.2−79.4 mm). Adult males were significantly larger than adult females ($P<0.0001$). Mean BW of adult males was 13.4 ± 5.0 g (n=396; range, 3.25−22.8 g) and that of adult females was 8.5 ± 2.5 g (n=183; range, 3.9−16.9 g). In addition, BW of adult males was significantly greater than that of adult females ($P<0.0001$).

Fig. 1. Swinhoe's tree lizard (*Diploderma swinhonis*) in Hyuga City. Male lizards (a) were larger than females (b). Mature male lizards also have a yellow stripe on their flanks. Bar=5 cm.

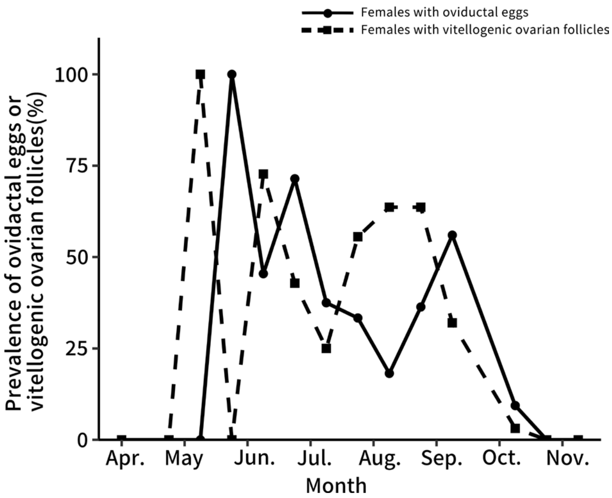

Fig. 2. Seasonal changes in the rate of *Diploderma swinhonis* females with oviductal eggs and vitellogenic ovarian follicles in Hyuga City.

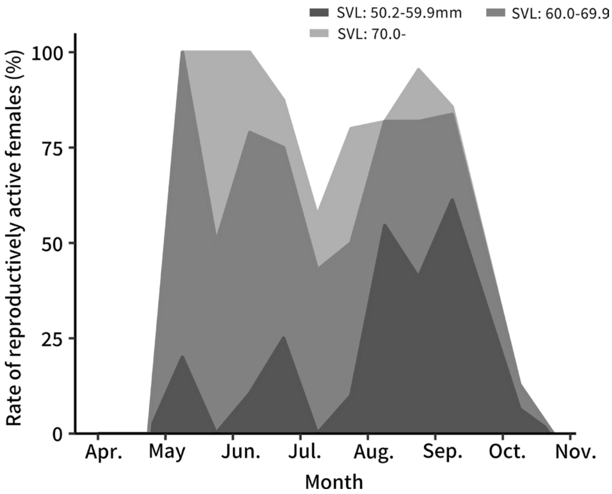

Fig. 3. Seasonal changes in the rate of reproductively active *Diploderma swinhonis* females in Hyuga City, Japan, as a function of snout–vent length (SVL). Dark-gray shading shows the number of females with SVL=50.2–59.9 mm, gray shading shows the number of females with SVL=60.0–69.9 mm. Light-gray shading shows the number of females with SVL ≥70.0 mm.

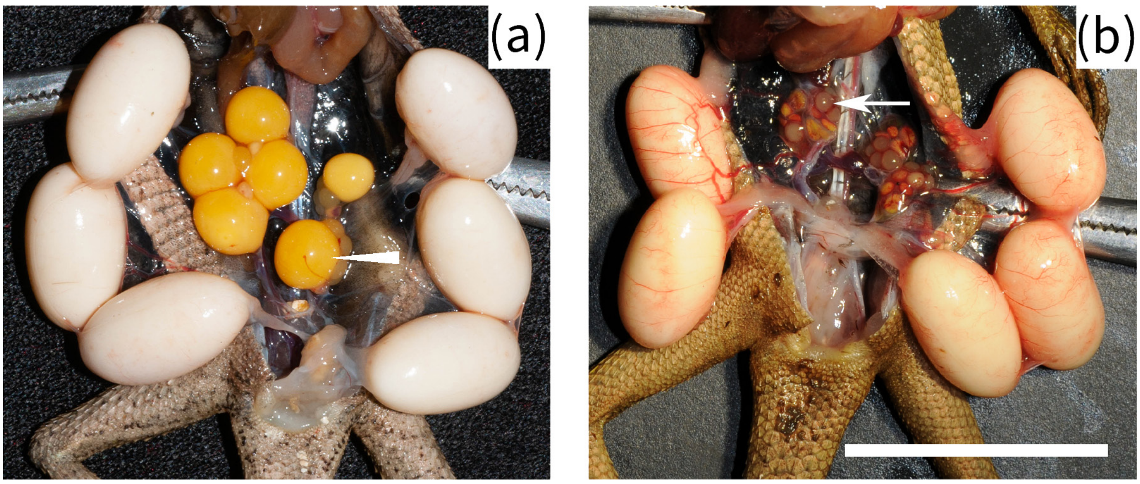

Fig. 4. Macroscopic image shows oviductal eggs and ovaries of *Diploderma swinhonis*. (a) A female that was captured in June had 6 oviductal eggs and 6 vitellogenic ovarian follicles (arrowhead). (b) A female that was captured in September had 5 oviductal eggs. Ovaries had only small ovarian follicles (arrow). Bar=2 cm.

Female reproductive cycle

The minimum SVL of *D. swinhonis* females with vitellogenic ovarian follicles and oviductal eggs was 50.2 mm and 50.8 mm, respectively. Consequently, female lizards with SVL greater than 50.2 mm were considered to be sexually mature. The earliest that vitellogenic ovarian follicles were observed was in early May (Fig. 2). All females had oviductal eggs by late May and most adult females were reproductively active from May to mid-October. Until July, large (SVL >70 mm) or medium-sized (60.0–69.9 mm SVL) females comprised the majority of reproductively active females, but the proportion of small females (50.0–59.9 mm SVL) that were reproductively active increased from August to September (Fig. 3). By late October, no females were reproductively active (Figs. 2 and 3). As shown in Fig. 2, there were three peaks in the presence of oviductal eggs. From May to July, many females with oviductal eggs also had enlarged yellow ovarian follicles. Seven females (28% of females captured from May to July) had both oviductal eggs and vitellogenic ovarian follicles (Fig. 4a). Other matured females with oviductal eggs had less than 3 mm in diameter of yellow ovarian follicles. From August to November, except two females, females with oviductal eggs had only translucent ovarian follicles that were less than 2 mm in diameter (Fig. 4b). The average number of oviductal eggs was 5.0 ± 1.4 (n=66; range, 2–8), and the average number of vitellogenic ovarian follicles was 5.0 ± 1.6 (n=69; range, 1–8). The average clutch size was 5.1 ± 1.5 (n=126; range, 2–8). In addition, there was a positive correlation between SVL and clutch size (y=0.16 × −4.9; r=0.69; n=126; *P*<0.0001).

Male reproductive cycle

The minimum SVL of *D. swinhonis* males with spermatozoa in seminiferous tubules was 45.2 mm. In addition, the minimum SVL of males with spermatozoa in epididymal ducts was 53.0 mm. Therefore, male lizards that were larger than 53.0 mm SVL were considered to be sexually mature, and testis size and SVL were positively correlated (y=1.8 × −72.1; r=0.65; n=154; *P*<0.0001). As shown in Fig. 5, testes size of large males (>70 mm SVL) showed seasonal change. Comparing each monthly averaged testes size of large males using Tukey-Kramer test, testes size in April, September and October had significant smaller than those in May, June, July and August (*P*<0.05). In addition, monthly-averaged testes size was lowest in September. Histological analysis showed seasonal changes in the spermatogenic epithelium as shown in Fig. 6. For example, in April, very few males had spermatozoa (2/10; 20%) (Fig. 6a), but from late May to August, spermatozoa were observed in the spermatogenic epithelium of all matured males (Fig. 6b). By September, the number of cells and thickness of spermatogenic epithelium had decreased significantly and cellular debris was observed in the seminiferous tubules (Fig. 6c), suggesting that testicular regression had occurred. In October and November, the number of cells and thickness of spermatogenic epithelium had increased compared to that observed in September (Fig. 6d), suggesting that testicular recrudescence may occur in this period. Spermatozoa were observed in the epididymides from May to November, but spermatozoa observed in the epididymides from September to November were less compare to other months.

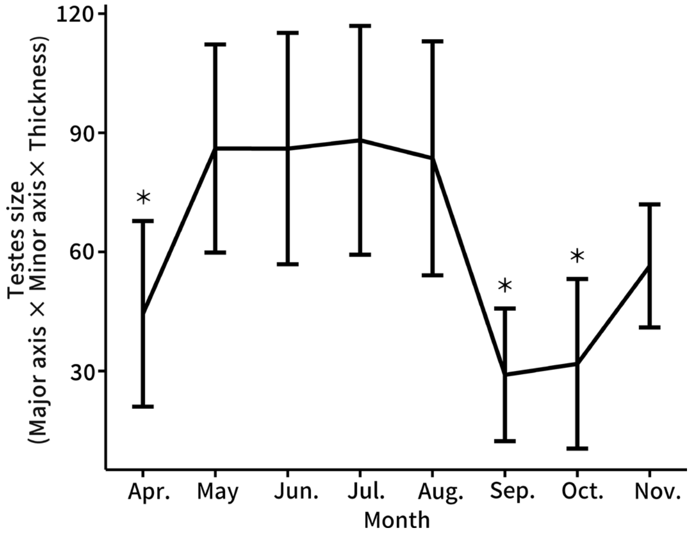

Fig. 5. Seasonal changes in testis size of *Diploderma swinhonis* in Hyuga City, Japan. Data show mean ± SD. * shows testes size in April, September and October had significant smaller than those in May, June, July and August (*P*<0.05).

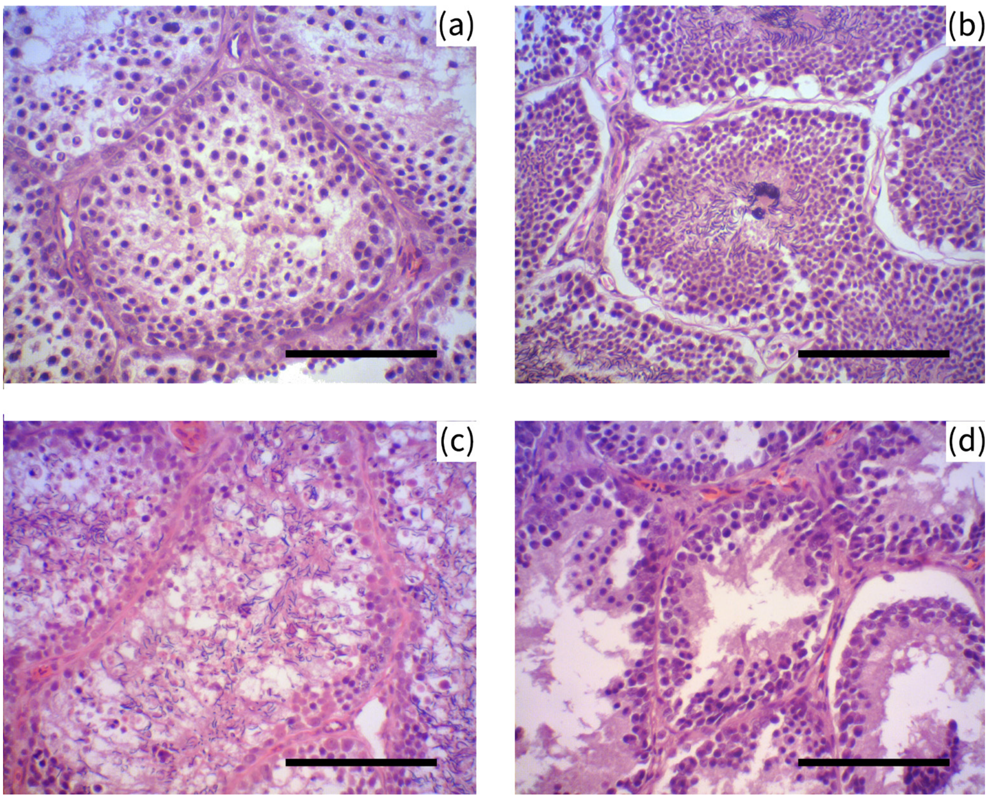

Fig. 6. Micrographs showing seasonal differences in the seminiferous tubules of *Diploderma swinhonis.* (a) In April, no spermatozoa were observed in seminiferous tubules. (b) In July, numerous spermatozoa were observed in spermatogenic epithelium. (c) In September, degenerating cells were observed in the spermatogenic epithelium. (d) In mid-October, the number of cells and thickness of spermatogenic epithelium increased. Bar=100 μm.

DISCUSSION

The findings of the present study show that *D. swinhonis* females in Hyuga City deposit their eggs from late spring to early autumn and that spermiogenesis in males occurs at approximately the same time. In addition, the presence of females with both vitellogenic ovarian follicles and oviductal eggs suggests the *D. swinhonis* in Hyuga City lay more than two clutches of eggs a year. Seasonal change of the presence rate of female with oviductal eggs suggest many of adult female oviposit twice from late of May to July and some oviposit once more from August to September (Fig. 2). The reproductive cycle of *D. swinhonis* in Hyuga City is thus similar to many temperate reptiles, including lizards that are native to Japan, which reproduce from spring to summer [5, 8, 27].

The *D. swinhonis* population investigated in this study was introduced into the temperate zone of Japan from subtropical and tropical zones in Taiwan. By examining the reproductive physiology of this species in Japan, we sought to clarify the effect of differences in climate and other environmental factors, such as food availability, on the reproductive cycle and maturation of this species. Specifically, we examined whether the differences between these two climatic zones were manifested as differences in gross morphology (mean SVL, BW of mature lizards, and minimum SVL at sexual maturity), reproductive period, clutch frequency, and clutch size.

Comparisons of gross morphology of specimens from Hyuga City and specimens in Taiwan showed that the mean SVL of mature lizards from Hyuga City was less than that of lizards in Taiwan (Table 1) [7, 23]. While the mean BW of mature males from Hyuga City was greater than that of specimens in Taiwan, adult females from Hyuga City weighed less than specimens in Taiwan. To consider the interaction between body size and BW, we used body mass index (BMI), as shown in Table 1. The BMI was calculated by dividing the square of the mean SVL by the mean BW, as described in a previous report [28]. The observation that *D. swinhonis* specimens from Hyuga City had a higher average BMI than specimens in Taiwan suggests that the nutritional status of the introduced *D. swinhonis* population in Hyuga City is better than that of lizards in Taiwan. The smaller mean SVL observed in lizards from Hyuga City is contrary to Bergman's rule, but exceptions to the rule have been reported in some ectothermal animals [21, 25, 32]. While the underlying reasons for such exceptions are not completely understood, it is reasonable to assume that a decrease in body size may be an adaptation to colder climates [21].

In addition, the minimum SVL at sexual maturity was smaller in the population from Hyuga City than that in specimens in Taiwan, as shown in Table 2 [7, 15, 16, 23]. Several studies have shown that lizards with short activity periods attain larger body size at sexual maturity because a larger body size at sexual maturity is caused by slow growth [1, 6]. Hibernation of *D. swinhonis* in Taiwan begins in November and ends in late February [9]. In Hyuga City, *D. swinhonis* was not observed from December to March and may have been hibernating during that time. Consequently, since the *D. swinhonis* population in Hyuga City appears to have a relatively longer hibernation period, the period over which it can capture prey and increase in size may be shorter than that of populations in Taiwan. The data discrepancy could be indicative of a better nutritional condition of the lizards in Hyuga City, in which the lizards have fast growth and early maturation.

Table 1. Snout-vent length, body weight and body mass index of mature *Diploderma swinhonis* in Japan and Taiwan

	Male			Female		
	SVL (mm)	BW (g)	BMI	SVL (mm)	BW (g)	BMI
Hyuga City (this study)	72.6 ± 7.7 (53.0 – 87.4)	13.4 ± 5.0 (3.25 – 22.8)	2.5	62.1 ± 6.2 (50.2 – 79.4)	8.5 ± 2.5 (3.9 – 16.9)	2.2
Orchid Island [9]	74.6 (62.1 – 81.9)	11.2 (6.2 – 15.3)	2.0	69.3 (63.3 – 76.3)	9.3 (6.8 – 12.1)	1.9
Southwest Taiwan [25]	N.D.	N.D.	N.D.	66.9 ± 2.3 (64.0 – 70.0)	8.9 ± 0.8 (7.5 – 10.1)	2.0

N.D.: no data, SVL: snout-vent length, BW: body weight, BMI: body mass index. Ranges of SVL and BW are shown in parentheses.

Table 2. Clutch size, clutch frequency, minimum snout-vent length at sexual maturity and reproductive period of *Diploderma swinhonis* in Hyuga City (Japan) and Taiwan

Location [Source]	Clutch size (eggs)	Clutch frequency (clutches/year)	Minimum SVL (mature lizards)		Reproductive period	
			Male	Female	Presence of oviductal eggs	Presence of spermatozoa in epididymides
Hyuga City (this study)	5.1 ± 1.4	2–3	53.0	50.2	May−Oct.	May−Nov.
Northwestern Taiwan [17]	4.3	N.D.	54.0	53.0	May−Sep.	Mar.−Aug.
Southern Taiwan [18]	4.6	2–3	63.0	56.0	Apr.−Sep.	Mar.−Aug.
Orchid Island [9]	3.3 ± 0.16	2–3	62.1	63.3	May−Oct.	N.D.
Southwestern Taiwan [25]	4.0 ± 0.91	N.D.	N.D.	64.0	Apr.−Sep.	N.D.

N.D.: no data, SVL: snout-vent length.

Assessments of reproductive period focused on two parameters: the presence of oviductal eggs in females, and spermatozoa in the epididymides of males, as shown in Table 2 [7, 15, 16, 23]. The onset and termination of the reproductive period was delayed in the Hyuga City population compared to the Taiwan populations, but the total length of the reproductive period was similar between regions. While the factors that regulate the seasonality of reproduction have not yet been accurately clarified in reptiles, breeding in the green anole (*Anolis carolinensis* (Voigt, 1832)) is regulated by complex interactions between temperature and day length [13, 14]. Although the differences in the onset of reproduction in *D. swinhonis* can be explained by differences in the climates of Japan and Taiwan, the termination of the reproduction period cannot be attributed to climatic factors. Therefore, further detailed studies are necessary in order to clarify which factors regulate seasonal reproduction in *D. swinhonis*.

The clutch size of the Hyuga City population was larger than that reported for populations in Taiwan, but clutch frequency did not differ between the regions (Table 2) [7, 15, 16, 23]. It has been reported that low temperatures decrease reproductive productivity [18], and that high latitudes and increased elevation can increase clutch size and decrease clutch frequency, respectively [19, 30]. In addition, nutritional status can also affect clutch frequency [3, 4, 31]. We consider that the combination of high nutritional status combined with favorable environmental conditions increased the clutch size of the lizards in Hyuga City.

The findings of this study also indicated that the *D. swinhonis* population in Hyuga City is a seasonal breeder and that these lizards mature earlier and have a larger clutch size than populations in Taiwan. Taken together, the results suggest that the population of *D. swinhonis* in Hyuga City will increase in the future, and that an extermination program is necessary in order to prevent range expansion of this species in Japan.

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