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Ecological Traits of a Common Japanese Pit Viper, the Mamushi (*Gloydius blomhoffii*), in Kyoto, with a Brief Geographic Comparison

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Abstract: *Gloydius blomhoffii* is a common pitviper distributed throughout Japan except for Okinawa Prefecture. To understand intraspecific geographic variation of this widely distributed snake, I describe several of its basic ecological traits observed during a 31-year-field survey conducted in the forest of Ashiu, northeastern Kyoto, in the western region of the mainland of Japan, and compare these traits with those reported in previous studies conducted in widespread areas of Japan. Body length of *G. blomhoffii* in Kyoto was smaller than that in the northernmost range and larger than that in the southernmost range. Sexual size dimorphism in snout-vent length, tail length, and body mass showed the same trends as in other areas. The sex ratio of the collected snakes was biased to females, which has not been observed in other studies. Pregnant females showed higher body temperature than males and non-pregnant females at a given air temperature. Parturition period, litter size, and body size of neonates generally overlapped with those reported in previous studies. Stomach contents were found only in 9.1% of snakes and consisted of rodents, frogs, and newts, which are prey items already known in *G. blomhoffii*. Although the forest in Ashiu has been incurred drastic environmental degradation, no obvious change in body size was detected over the study period. This study adds information on ecological traits of *G. blomhoffii* based on a population-level study and will facilitate future intensive field research to understand this common, but still poorly investigated, venomous snake endemic to Japan.

Key words: Activity pattern; Body temperature; Diet; Reproduction; Sexual size dimorphism

INTRODUCTION

Investigations of intraspecific variation among different populations provide important clues to understand the evolutionary mechanisms of phenotypic traits of animals. Different environmental conditions in geographically remote areas can induce phenotypic variation among a species (Schlichting and Pigliucci, 1998; Foster and Endler, 1999). Elucidation of factors that have caused such intraspecific variation is one

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of the ultimate goals in evolutionary biology. The essential first step toward this goal is, however, to clarify and describe the pattern of intraspecific geographic variation. Widely distributed species are, therefore, ideal subjects to untangle the complex process of the phenotypic evolution.

Gloydius blomhoffii is a common, geographically widespread venomous snake in Japan, distributed in all main islands (Hokkaido, Honshu, Shikoku, and Kyushu) and their adjacent islands, covering various habitats from the subfrigid to temperate climatic zones (Gloyd and Conant, 1990; Goris and Maeda, 2004). *Gloydius blomhoffii* is a pit viper endemic to Japan and is a well-known snake even to local people because of the frequent occurrences of human envenomation in rural areas (Okamoto et al., 2017; Chiba et al., 2018). Accordingly, numerous studies on the toxicity of its venom and medical treatments have been reported (e.g., Hifumi et al., 2011, 2015; Taki et al., 2014; also see references in Toriba and Sawai, 1990). In contrast, basic ecological studies in the field, particularly population-level studies such as Kadowaki (1996) and Mori and Nagata (2016), are quite limited, in spite of the species' apparent familiarity to biologists and its potential importance for applied medical sciences.

During a long-term ecological study on diurnal colubrid snakes conducted in Kyoto, western Honshu area, I had a number of opportunities to encounter *G. blomhoffii* and to record some of its ecological traits. In this study, I present basic data on body size, monthly and daily activity patterns, thermal and reproductive characteristics, and diet of *G. blomhoffii* collected over 30 years. Then, I briefly compare these traits with those reported in previous studies conducted in its northernmost and southernmost geographic ranges, Hokkaido (Sasaki et al., 2008, 2012) and southern Kyushu (Yomeishu Seizo Co., Ltd., 1999), respectively, and in the eastern side of its central geographical range, Tsukuba (Kadowaki, 1996). Here, I provide basic ecological features of a population in the western side of the central range of *G. blomhoffii* and briefly analyze the pattern of geographic variation in the species, observed over the environmentally diverse Japanese islands.

Materials and Methods

The study site (35°18'N, 135°43'E) is located in the northeastern area of Kyoto Prefecture, Japan, close to the borders with Shiga and Fukui Prefectures. The study was conducted in the Ashiu Forest Research Station of the Field Science Education and Research Center, Kyoto University and in adjacent paddy fields owned by local residents. The elevation of the study area ranges from 355 to 688 m. Air temperature of the study site is lowest in January (the average air temperature is 0°C), and highest in August (the average air temperature is 25°C). The Yura River runs across the study site, and many small streams flow into the river. The study site consists of hilly terrain, and most areas are covered with dense forest consisting mainly of *Aesculus turbinata*, *Pterocarya rhoifolia*, *Quercus cripula*, *Q. salicina*, and coniferous plantation (mostly *Cryptomeria japonica*). Grasslands dominated by *Miscanthus* and *Phragmites* are scattered in open flat areas along the banks of the river. There is a small hiking trail along the river that extends more than 5 km.

The field survey was conducted mainly along the hiking trail and in and around the nearby paddy fields between April and October, from 1989 to 2020. The frequency of the survey varied year to year. I haphazardly walked along the survey area basically between 0800 h and 1800 h, and occasionally at dusk and night between 1700 h and 0300 h. Hence, research efforts were not constant nor controlled over months, hours, or areas. Therefore, I avoided analyzing data that are biased by these restrictions (see Results). I attempted to collect snakes whenever I found them on the surface. I did not collect snakes hiding themselves in shelters. Immediately after a snake was collected, I measured cloacal body temperature to the nearest 0.1°C with a thermistor (Takara, Digimulti D611 or Sato, Sk-1260). The ambient air temperature at 1 m above the ground (AT) (in shade in case of daytime) and the substrate temperature (ST) of the site, at which the snake was first observed were also measured. Sunlight exposure of the snake's body was recorded either as full sun, filtered sun, or shade. The snake was brought to the field station, and snout-vent length (SVL), tail length (TaL), and body mass (BM) were measured, and its sex was determined by examining the external shape of the tail base or by everting hemipenes. Reproductive condition of females (pregnant or non-pregnant) was determined by gentle palpation of the ventral side of the posterior part of the body. Stomach contents were detected by gentle palpation and were recovered by force-regurgitation.

I did not release the snakes because it was either not allowed by local land owners or not recommended by the Ashiu Forest Research Station, due to the possibility of snake bites to local residents or hikers by the released snakes. Thus, all collected snakes were brought back to the laboratory at Kyoto University for behavioral experiments or for preservation and deposit in the Kyoto University Museum. Reproductive condition and stomach contents of some individuals were examined by the dissection of the preserved specimens. Because of occasional logistic limitations related to the handling of venomous snakes, I was not able to record all variables described above for each snake, and thereby sample size varies depending on analyses. If females gave birth in the laboratory, I measured SVL, TaL, and BM of neonates and determined their sex, if possible.

Sexual differences in SVL were examined using Student t-test. Relative TaL and BM was compared between the sexes using ANCOVA with SVL as covariate. Because of the small range of SVL and high linear correlation coefficients of SVL with TaL and BM, I did not log-transform the data for ANCOVA. Paired t-test was used to compare BT with corresponding AT and ST. BT was compared among males, pregnant females, and non-pregnant females using ANCOVA with AT or ST as covariate. In ANCOVA only the results of elevation are shown because significant effects in slope were not detected in any comparison. Sex ratio of collected snakes was examined using the Binomial test. Differences in activity time (day or night) and sunlight condition between the sexes was examined using the Fisher exact test. All statistical analyses were conducted using JMP Pro (ver. 15.1.0), with a significance level of $P=0.05$. To examine a possible long-term change in body size, which could be caused by environmental changes in the study site (e.g., Kato and Okuyama, 2004; Fukushima and Tokuchi, 2008), the survey period was divided into three decades (1989–2000, 2001–2010, and 2011–2020), and SVL was compared among these periods.

Results

In total, 16 males and 53 females were collected. This sex ratio was significantly biased from 1:1 (Binomial test, $P<0.0001$). The earliest and latest dates I collected *G. blomhoffii* were 30 April and 12 October, respectively (both were females). The monthly pattern of fluctuation in the number of collected snakes was similar in males and females (Table 1). Pregnant females were collected from 6 May to 9 October. Overall, 61.0% of females were determined to be pregnant (Table 1). Eleven of 16 males were collected during the day (0800–1700 h), whereas 41 of 49 females were collected during the day (Table 2). Females tended to be collected more frequently during the day than at dusk or at night (1700–0300 h) compared to males, but the difference was not significant (Fisher exact test, $P=0.279$). There was also no significant difference in the activity times of pregnant and non-pregnant females ($P=0.658$).

TABLE 1. The number of *Gloydius blomhoffii* collected each month. PF: pregnant female, NPF: non-pregnant female, NDF: female for which reproductive condition was not determined.

Sex	Month							Total
	Apr	May	Jun	Jul	Aug	Sep	Oct	
Male	0	2	6	3	2	3	0	16
Female	1	8	17	8	5	11	3	53
PF	0	1	6	6	2	8	2	25
NPF	0	4	8	1	0	2	1	16
NDF	1	3	3	1	3	1	0	12

TABLE 2. The number of *Gloydius blomhoffii* collected during each time period of the day. PF: pregnant female, NPF: non-pregnant female, NDF: female for which reproductive condition was not determined.

Sex	Time of day										Total
	7–9	9–11	11–13	13–15	15–17	17–19	19–21	21–23	23–1	1–3	
Male	1	2	3	3	2	1	3	0	1	0	16
Female	2	13	14	9	3	4	1	2	0	1	49
PF	2	9	2	6	2	2	1	0	0	0	24
NPF	0	2	8	2	0	0	0	2	0	1	15
NDF	0	2	4	1	1	2	0	0	0	0	10

Females were significantly larger than males in SVL (t-test, t=2.36, df=52, P=0.0218; Table 3). SVL of pregnant females completely overlapped with that of non-pregnant females (range, 420–522 mm and 442–502 mm in pregnant and non-pregnant females, respectively; Table 3). Relative TaL was significantly larger in males than in females (ANCOVA, F=92.2, df=1, 53, P<0.0001). Relative BM was significantly larger in females (all individuals combined) than in males (ANCOVA, F=8.02, df=1, 50, P=0.0067). Relative BM of pregnant females was significantly larger than that of males (ANCOVA, F=26.2, df=1, 29, P<0.0001), but there was no significant difference in relative body mass between non-pregnant females and males (ANCOVA, F=0.005, df=1, 22, P=0.946).

Among 15 males, three individuals were observed in full sun and the remaining 12 were sighted in shade. Among pregnant females, five, three, and 14 individuals were observed in full sun, filtered sun, and shade, respectively. Of the non-pregnant females, two, three, and nine individuals were observed in full sun, filtered sun, and shade. The proportion of snakes observed in sunlight (full sun or filtered sun) was not significantly different among males, pregnant females, and non-pregnant females (20%, 36.4%, and 35.7%, respectively; Fisher exact test, P=0.553).

Mean BT of males, pregnant females, and non-pregnant females were 22.6°C, 25.8°C, and 23.8°C, respectively (Table 4). In males and pregnant females BT was significantly higher than corresponding AT and ST (paired t-test; males, AT vs. BT, t=2.6, df=10, P=0.0402, ST vs. BT, t=3.5, df=10, P=0.0072; pregnant females, AT vs. BT, t=6.1, df=19, P<0.0001, ST vs. BT, t=4.0, df=19, P=0.0008), whereas in non-pregnant females there was no significant difference

TABLE 3. Mean±SE of body size measurements of *Gloydius blohmhoffii* in Kyoto. Sample size and range are shown in parentheses. SVL: snout-vent length, TaL: tail length, ToL: total length, BM: body mass. ToL is shown to facilitate comparison with previous studies.

Variable	Male	Female		
		All	Pregnant female	Non-pregnant female
SVL	443.6±27.3 (14, 370–475)	461.4±22.2 (44, 420–522)	464.1±25.0 (21, 420–522)	462.1±18.7 (12, 442–502)
TaL	93.1±6.3 (14, 78–101)	82.0±4.8 (43, 74–92)	82.4±4.8 (21, 74–92)	81.3±5.8 (12, 75–92)
ToL	538.2±31.6 (15, 448–569)	542.4±26.5 (44, 477–614)	546.5±27.6 (21, 501–614)	543.4±21.9 (12, 518–588)
BM	65.0±11.3 (15, 42–86)	86.7±20.8 (41, 46–146)	97.7±18.8 (20, 70–146)	75.8±19.1 (12, 46–108)

TABLE 4. Mean±SE of body temperature (BT) of *Gloydius blohmhoffii* and corresponding air temperature (AT) and substrate temperature (ST). Sample size and range are shown in parentheses.

	Male	Female		
		All	Pregnant female	Non-pregnant female
BT	22.6±3.5 (11, 17.4–28.7)	24.8±4.1 (37, 12.0–31.5)	25.8±3.6 (20, 18.6–31.5)	23.8±5.3 (8, 12.0–30.2)
AT	21.5±3.4 (11, 17.1–28.5)	21.9±3.7 (37, 11.3–29.2)	21.4±3.2 (20, 16.0–26.4)	22.1±4.8 (8, 11.3–27.3)
ST	20.6±4.1 (11, 14.7–29.0)	23.5±4.8 (37, 11.7–35.7)	23.8±4.5 (20, 16.2–35.7)	22.4±5.5 (8, 11.7–31.2)

either between AT and BT or between ST and BT (former, t=1.6, df=7, P=0.1640; latter, t=2.3, df=7, P=0.0527). BT was significantly correlated with both AT and ST in males, pregnant females, and non-pregnant females (AT, males, r^2=0.79, F=34.54, df=1, 9, P=0.0002, pregnant females, r^2=0.30, F=7.77, df=1, 18, P=0.0121, non-pregnant females, r^2=0.66, F=11.68, df=1.6, P=0.0142; ST, males, r^2=0.74, F=25.69, df=1, 9, P=0.0007, pregnant females, r^2=0.74, F=52.21, df=1, 18, P<0.0001, non-pregnant females, r^2=0.90, F=54.55, df=1.6, P=0.0003). There were significant differences in elevation of regression lines between AT and BT among these three sex/reproduction categories (ANCOVA, F=5.47, df=2, 33, P=0.0089). Paired comparisons showed significantly higher BT in pregnant females than in males and non-pregnant females (former, F=10.38, df=1, 28, P<0.0001; latter F=3.75, df=1, 25, P=0.0001) and no significant difference between males and non-pregnant females (F=0.31, df=1, 16, P=0.5849). On the other hand, there was no significant difference in elevation of regression lines between ST and BT among the three sex/reproduction categories (ANCOVA, F=1.07, df=2, 33, P=0.3559).

Although sample sizes were small, mean SVLs were similar throughout the three decadal periods in both sexes. In males, mean SVL of the earliest, middle, and latest periods were 439.2 mm (n=6), 438.0 mm (n=3), and

TABLE 5. Details for snakes that contained stomach contents. SVL: snout-vent length.

Sex	Reproductive condition	Date	SVL	Stomach contents	Collection site
Male	na	20 May 1990	560*	Rodent	Dry river bed
Male	na	14 Sep 1994	410	*Apodemus argenteus*	Hiking trail on mountain ridge
Female	non-pregnant	2 May 1996	ca. 425**	*Cynops pyrrhogaster*	Paddy field
Female	unknown	23 May 1996	440	*Zhangixalus schlegelii*	Hiking trail along the river
Female	non-pregnant	12 Oct 2009	447	*Rana tagoi*	Hiking trail along the river
Female	pregnant	14 Jun 2018	481	*Cynops pyrrhogaster*	Paddy field

* Total length.
** Measurement of preserved specimen.

452.2 mm (n=5), respectively, and in females those were 460.4 mm (n=28), 466.2 mm (n=10), and 457.8 mm (n=6), respectively.

Stomach contents were found only in two out of 16 males and four out of 50 females (9.1% in total). Both males, which were collected in May and September each, contained rodents, and all four females contained amphibians, including two frogs and two newts (Table 5).

Ten females gave birth to neonates in the laboratory between 17 September and 20 October. Litter size varied from 2–6 (mean=4.0, including still-born neonates). Mean±SE of SVL, TaL, and BM of neonates were 183.4±10.2 (n=14), 42.1±3.1 (n=14), and 5.9±0.9 (n=14) for males, and 181.4±9.4 (n=10), 35.7±2.5 (n=10), and 5.9±1.1 (n=10) for females, respectively (sex of 16 neonates was not determined). Relative TaL was significantly larger in males than in females (ANCOVA, $F=76.6$, $df=1, 20$, $P<0.0001$).

DISCUSSION

Sexual size dimorphism observed in this study agrees with the general trend reported in previous studies of *G. blomhoffii* conducted in various areas: females have larger SVL and larger relative BM than males, and males have longer relative TaL than females (Uchida and Imaizumi, 1939; Kadowaki, 1996; Yomeishu Seizo Co., Ltd., 1999; Sasaki et al., 2012; Mori and Nagata, 2016). A previous study conducted in Hokkaido showed, by comparison with studies in two southern areas, that adults are larger in northernmost populations than in southern Japan (Sasaki et al., 2012). A comparison of the present data with those previously reported from seven other areas partially supports this tendency: largest body size in the northernmost area and smallest body size in the southernmost area (Table 6). However, the trend does not necessarily show a clear latitudinal gradation, and especially on Honshu, the mainland of Japan, the pattern of geographic variation does not seem simple. For example, *G. blomhoffii* in Aomori and Kyoto, which are separated from each other by more than 800 km in straight distance, exhibit similar body sizes, whereas *G. blomhoffii* on Kinkasan Island have larger body size compared to those of the close mainland area, Aomori. Intraspecific variation in body size is a well-known phenomenon in snakes (e.g., Boback, 2003), and such variation would reflect differences in longevity, plastic responses in growth to local environments, or local adaptation (Hasegawa and Mori, 2008). Obviously, more intensive, comparative field studies focusing on locally characteristic environments are required to elucidate the proximate and ultimate factors underlying geographic body size variation of *G. blomhoffii*.

Although my survey efforts were not constant across months and previous studies employed various survey methods, the active

TABLE 6. Comparison of mean body length (SVL: snout-vent length, ToL: total length) of *Gloydius blomhoffii* among areas thoughout its geographical range. Hokkaido and southern Kyushu are its northernmost and southernmost geographical ranges, respectively. Areas are listed from left to right in order of their approximate geographic position from north to south. Numbers in parentheses are sample sizes.

Variable		Study area							
		Hokkaido	Aomori*	Miyagi** (Kinkasan Island)	Tsukuba**	Kansai	Kyoto**	Hiroshima	Southern Kyushu
Latitude (N)		ca. 43°	ca. 41°	38°43'	36°8'	ca. 35°	35°18'	ca. 34–35°	ca. 31–32°
Longitude (E)		ca. 141°	ca. 141°	141°31'	140°2'	ca. 136°	135°43'	ca. 133°	ca. 131°
Male	SVL	482–523 (76)	439 (42)	498 (9)	412 (60)	—	444 (14)	431 (13)	—
	ToL	—	—	—	—	550 (ca. 20)	538 (15)	—	494 (1314)
Female	SVL	496–551 (216)	467 (42)	514 (16)	462 (50)	—	461 (44)	430 (14)	—
	ToL	616 (217)	—	—	—	600 (ca. 20)	542 (44)	—	497 (873)
Reference		Sasaki, 2006; Sasaki et al. 2012	Uchida and Imaizumi, 1939	Mori and Nagata, 2016	Kadowaki, 1996	Fukada, 1992	This study	Okawa, 2002	Yomeishu Seizo Co., Ltd., 1999

* A few snakes collected in other areas may be included.
** Study of a single population.

season of *G. blomhoffii* in my study site generally agrees to that in other areas, i.e., activity from late April to October (Uchida and Imaizumi, 1939; Kadowaki, 1996; Okawa, 2002), although in its southernmost range the snake has been reported to be active until mid-November (Yomeishu Seizo Co., Ltd., 1999). Anecdotal descriptions often mention that *G. blomhoffii* is primarily nocturnal, and diurnal activity mostly reflects basking by pregnant females to raise the developmental temperature of their embryos (e.g., Toriba, 1996). However, there is no behavioral study that tracks the actual activity pattern of individual snakes. Because I conducted the survey primarily during the day, the higher proportion of females than males observed in my study site may reflect the frequent basking behavior of pregnant females. Nonetheless, my observation of males and non-pregnant females in the day throughout the study period indicates that diurnal activity is not limited to pregnant females in summer. Actually, despite the fact that previous field studies on *G. blomhoffii* were primarily conducted during the day (Kadowaki, 1996; Sasaki et al., 2008; Mori and Nagata, 2016), sex ratios at their study sites were not highly biased toward females. Furthermore, the low proportion of the pregnant females observed in sunlight (36.4%) implies that their diurnal activity is not restricted to the basking purpose. These lines of evidence suggest that *G. blomhoffii* as a whole is more active in the day than previously believed. On the other hand, pregnant females maintained BT higher than males and non-pregnant females at a given AT, although BT is highly correlated with ambient temperatures in all three groups. A similar trend was observed in *G. blomhoffii* in the Tsukuba population (Kadowaki, 1996), suggesting that pregnant *G. blomhoffii* thermoregulates more precisely than males and non-pregnant females, as in many other viviparous snakes (e.g., Peterson et al., 1993; Wittenberg, 2017). Again, individually based research, such as a radio-tracking study, will be essential to clarify the activity pattern and thermoregulatory behavior of *G. blomhoffii*.

The proportion of pregnant females between June and August, when the presence of embryos in the female's abdomen is accurately determined by palpation, was 60.3% (14/23) in my study site. Previous studies show that this proportion varies year to year from 0.27 to 0.59 (Sasaki et al., 2012), from 0.40 to 0.82 (Kadowaki, 1996), and from 0.24 to 0.53 (Yomeishu Seizo Co., Ltd., 1999) in Hokkaido, Tsukuba, and southern Kyushu, respectively. Parturition period of *G. blomhoffii* at my study site (17 September to 20 October) largely overlaps with that in Hokkaido (12 September to 24 October; Sasaki et al., 2012), Kansai (31 August to 14 October; Fukada, 1962), and southern Kyushu (late August to early October; Yomeishu Seizo Co., Ltd., 1999) despite the obvious climatic differences among these study areas. Body size of neonates and litter size are also similar to those reported in previous studies (see summary Table 2 in Sasaki et al., 2012) although mean litter size in the present study (4.0) seems slightly smaller (6.6, 3.6, 5.5, and 4.6 in Hokkaido, Tsukuba, Kansai, and southern Kyushu, respectively; Fukada, 1962; Kadowaki, 1996; Yomeishu Seizo Co., Ltd., 1999; Sasaki et al., 2012). In general, these reproductive traits of snakes are influenced by many intrinsic and extrinsic factors, such as size and nutrient conditions of females and environmental thermal conditions (Seigel and Ford, 1987; Ford and Seigel, 2011). Thus, geographic effects, even if present, would not be easily detected by a simple comparison among populations. In the future, multivariate analysis approaches coupled with controlled laboratory experiments would be helpful for revealing exclusively geographic effects on reproductive characteristics of *G. blomhoffii*.

Gloydius blomhoffii is a generalist feeder, eating on a variety of vertebrates and some invertebrates, such as centipedes (Mori and Moriguchi, 1988; Hamanaka et al., 2014). All four prey species identified in the present study have been reported previously in the diet of *G. blomhoffii*. Although the sample size is quite small, it should be noted that one-third of the prey items were newts, *Cynops pyrrhogaster*, which has a highly toxic defensive chemical, tetrodotoxin, in its body (Wakely et al., 1966; Brodie et al., 1974). Exploitation of newts by *G. blomhoffii* has been reported in other areas (Mori and Moriguchi, 1988; Yomeishu Seizo Co., Ltd., 1999; Hamanaka et al., 2014), implying that this snake has physiological tolerance against tetrodotoxin. The relatively low proportion of snakes that contained stomach contents (9.1%) may reflect the ambushing foraging mode employed by *G. blomhoffii*, because sit-and-wait predators generally show low feeding frequency compared to active foragers (Huey and Pianka, 1981). Nonetheless, this value is lower than that of *G. blomhoffii* on Kinkasan Island (26.5%), the only available comparable information for this snake. Investigation of the foraging strategy of *G. blomhoffii* is another important issue to clarify in order to understand its plasticity and possible adaptation to local food resources.

During the last several decades the environments of the Ashiu forest have been drastically altered by the extensive increase in the population density of deer (*Cervus nippon*) (e.g., Kato and Okuyama, 2004; Fukushima and Tokuchi, 2008), as well as the loss of local paddy fields (Mori, personal observation) and possible climate change due to the global warming. These drastic environmental changes may have affected basic ecological traits, such as growth, reproduction, and population dynamics of wild animals living in this forest (e.g., Kato and Okuyama, 2004; Sakai et al., 2012; Nakagawa, 2019). Fortunately, I did not detect any obvious change in adult body size of *G. blomhoffii* during this 31-year-research period. Continuous monitoring of this population as well as comparative studies in other areas are strongly desired in order to clarify temporal and spatial ecological responses of *G. blomhoffii* to different environments. This could reveal possible ecological versatility, plasticity, and local adaptation of *G. blomhoffii*, which has been evolving in various environments over Japan. Further intensive field studies are crucial to understand this culturally well-known, but ecologically poorly understood, venomous snake.

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Literature Cited

Boback, S. M. 2003. Body size evolution in snakes: Evidence from island populations. *Copeia* 2003: 81–94.

Brodie, E. D., Jr., Hensel, J. L., and Johnson, J. A. 1974. Toxicity of the urodele amphibians *Taricha*, *Notophthalmus*, *Cynops* and *Paramesotriton* (Salamandridae). *Copeia* 1974: 506–511.

Chiba, T., Koga, H., Kimura, N., Murata, M.,

JINNAI, S., SUENAGA, A., KOHDA, F., AND FURUE, M. 2018. Clinical condition and management of 114 Mamushi (*Gloydius blomhoffii*) bites in a general hospital in Japan. *Internal Medicine* 57: 1075–1080.

FORD, N. B. AND SEIGEL, R. A. 2011. Offspring size variation in snakes. p. 573–586. *In*: R. D. Aldridge and D. M. Sever (eds.), *Reproductive Biology and Phylogeny of Snakes*. Science Publishers, Enfield.

FOSTER, S. A. AND ENDLER, J. A. 1999. *Geographic Variation in Behavior. Perspectives on Evolutionary Mechanisms*. Oxford University Press, New York.

FUKADA, H. 1962. Biological studies on the snakes IX. Breeding habits of *Agkistrodon halys blomhoffii* (Boie). *Bulletin of the Kyoto Gakugei University, Series B*. (20): 12–17.

FUKADA, H. 1992. *Snake Life History in Japan*. Impact Shuppankai Co. Ltd., Tokyo.

FUKUSHLMA, K. AND TOKUCHI, N. 2008. The influences of deer overbrowsing on nutrient cycling in forest ecosystems: Preliminary study of streamwater chemistry. *Forest Research* 77: 77–87.

GLOYD, H. K. AND CONANT, R. 1990. *Snakes of the Agkistrodon Complex. A Monographic Review*. Society for the Study of Amphibians and Reptiles, Oxford.

GORIS, R. C. AND MAEDA, N. 2004. *Guide to the Amphibians and Reptiles of Japan*. Krieger Publishing Company, Malabar.

HAMANAKA, K., MORI, A., AND MORIGUCHI, H. 2014. Literature survey on food habit of snakes in Japan: Revisited. *Bulletin of the Herpetological Society of Japan* 2014: 167–181.

HASEGAWA, M. AND MORI, A. 2008. Does a gigantic insular snake grow faster or live longer to be gigantic? Evidence from a long-term field study. *South American Journal of Herpetology* 3: 145–154.

HIFUMI, T., SAKAI, A., KONDO, Y., YAMAMOTO, A., MORINE, N., ATO, M., SHIBAYAMA, K., UMEZAWA, K., KIRIU, N., KATO, H., KOIDO, Y., INOUE, J., KAWAKITA, K., AND KURODA, Y. 2015. Venomous snake bites: Clinical diagnosis and treatment. *Journal of Intensive Care* 3: 16.

HIFUMI, T., YAMAMOTO, A., MOROKUMA, K., OGASAWARA, T., KIRIU, N., HASEGAWA, E., INOUE, J., KATO, H., KOIDO, Y., AND TAKAHASHI, M. 2011. Surveillance of the clinical use of Mamushi (*Gloydius blomhoffii*) antivenom in tertiary care centers in Japan. *Japanese Journal of infectious Diseases* 64: 373–376.

HUEY, R. B. AND PIANKA, E. R. 1981. Ecological consequences of foraging mode. *Ecology* 62: 991–999.

KADOWAKI, S. 1996. Ecology of a Japanese snake community—Resource use patterns of the three sympatric snakes, *Rhabdophis tigrinus*, *Elaphe quadrivirgata* and *Agkistrodon b. blomhoffii*—. *Bulletin of Tsukuba University Forests* 12: 77–148.

KATO, M. AND OKUYAMA, Y. 2004. Changes in the biodiversity of a deciduous forest ecosystem caused by an increase in the Sika deer population at Ashiu, Japan. *Contributions from the Biological Laboratory, Kyoto University* 29: 437–448.

MORI, A. AND MORIGUCHI, H. 1988. Food habits of the snakes in Japan: A critical review. *Snake* 20: 98–113.

MORI, A. AND NAGATA, E. 2016. Relying on a single anuran species: Feeding ecology of a snake community on Kinkasan Island, Miyagi Prefecture, Japan. *Current Herpetology* 35: 106–114.

NAKAGAWA, M. 2019. Habitat changes and population dynamics of fishes in a stream with forest floor degradation due to deer overconsumption in its catchment area. *Conservation Science and Practice* 1: e71.

OKAMOTO, O., NAKASHIMA, R., YAMAMOTO, S., HASHIMOTO, T., TAKASAKI, T., TOKUDA, H., SATO, S., GAMACHI, A., HASHIMOTO, H., AND INAGAKI, N. 2017. A lethal case of mamushi (*Gloydius blomhoffii*) bite: Severe bowel symptoms as a lethal sign. *Acute Medicine & Surgery* 4: 135–139.

OKAWA, H. 2002. A list of snake in Hiroshima Prefecture. *Journal of the Hiba Society of Natural History* 204: 1–18.

PETERSON, C. R., GIBSON, A. R., AND DORCAS, M. E. 1993. Snake thermal ecology: The causes and consequences of body-temperature vatiation. p.

241–314. *In*: R. A. Seigel and J. T. Collins (eds.), *Snakes. Ecology & Behavior*. McGraw-Hill, Inc., New York.

Sakai, M., Natuhara, Y., Imaniishi, A., Imai, K., and Kato, M. 2012. Indirect effects of excessive deer browsing through understory vegetation on stream insect assemblages. *Population Ecology* 54: 65–74.

Sasaki, K. 2006. Ecology, Behavior and Conservation of the Japanese Mamushi Snake *Gloydius blomhoffii*: Variation in Compromised and Uncompromised Populations. *Unpublished doctoral dissertation*. Oklahoma State University, Stillwater.

Sasaki, K., Fox, S. F., and Duvall, D. 2008. Rapid evolution in the wild: Changes in body size, life-history traits, and behavior in hunted populations of the Japanese Mamushi snake. *Conservation Biology* 23: 93–102.

Sasaki, K., Fox, S. F., and Duvall, D. 2012. Reproductive ecology and human-caused mortality in the Japanese Mamushi snake (*Gloydius blomhoffii*) on the northernmost main island of Japan. *Journal of Herpetology* 46: 689–695.

Schlichting, C. D. and Pigliucci, M. 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer Associates, Inc., Publishers, Sunderland.

Seigel, R. A. and Ford, N. B. 1987. Reproductive ecology. p. 210–252. *In*: R. A. Seigel and J. T. Collins (eds.), *Snakes. Ecology & Behavior*. McGraw-Hill, Inc., New York.

Taki, K., Ariyoshi, K., Sakai, A., Ishikawa, H., Nakashima, K., and Endoh, Y. 2014. Analysis of viper bites by the national survey. *Journal of Japanese Society for Emergency Medicine* 17: 753–760.

Toriba, M. 1996. Mamushi, Habu, and Benihebi. p. 101–105. *In*: S. Sengoku, T. Hikida, M. Matsui, and K. Nakaya (eds.), *The Encyclopaedia of Animals in Japan. Volume 5. Amphibians, Reptiles, Chondrichtheys*. Heibonsha, Tokyo.

Toriba, M. and Sawai, Y. 1990. Venomous snakes of medical importance in Japan. p. 323–347. *In*: P. Gopalakrishnakone and L. M. Chou (eds.), *Snakes of Medical Importance*. Venomous and Toxin Research Group, National University of Singapore, Singapore.

Uchida, K. and Imaizumi, Y. 1939. On the food habits of snakes. *Animal Survey Reports* 9: 143–208.

Wakely, J. F., Fuhrman, G. J., Fuhrman, F. A., Fischer, H. G., and Mosher, H. S. 1966. The occurrence of tetrodotoxin (tarichatoxin) in amphibia and the distribution of the toxin in the organs of newts (*Taricha*) *Toxicon* 3: 195–203.

Wittenberg, R. D. 2017. Thermal ecology of the timber rattlesnake (*Crotalus horridus*) in a fragmented agricultural landscape. p. 85–95. *In*: M. J. Dreslik, W. K. Heyes, S. J. Beaupre, and S. P. Mackessy (eds.), *The Biology of Rattlesnakes II*. ECO Herpetological Publishing and Distribution, Rodeo.

Yomeishu Seizo Co., Ltd. 1999. *Ecology and Artificial Propagation of the Mamushi*. Central Research Laboratories, Yomeishu Seizo Co., Ltd., Nagano.

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