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Change in the Guild Structure of a Snake Community in Japan over 30 Years

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Abstract: Long-term field studies have provided evidence of worldwide declines in vertebrate populations, including amphibians and reptiles. However, studies investigating the decline in snake populations are scarce. As obligate predators, snakes play important roles in local ecosystems and are in turn affected by their food resources. In the present study we investigated the seasonal abundance of snakes and their food habits in a rice paddy field and compared the results of the present study with those of a previous study that was conducted at the same site approximately 30 years ago. Our results showed that *Elaphe quadrivirgata*, a dietary generalist snake that had been one of the dominant species at the site, has drastically declined and that *Rhabdophis tigrinus* and *Gloydius blomhoffii* have remained as dominant species. Furthermore, in the present study, most of the stomach contents of *R. tigrinus* consisted of the Japanese tree frog, *Dryophytes japonicus*, whereas three frog species, *D. japonicus*, *Rana japonica*, and *Pelophylax porosus porosus*, had been the main prey of *R. tigrinus* 30 years ago. In addition, fewer individuals of *R. tigrinus* and *G. blomhoffii* contained food in their stomachs than 30 years ago. Our findings imply that a change in prey availability may have affected the guild structure of snakes at this study site, although further investigation is necessary to verify the reasons for the decline of the dietary generalist, *E. quadrivirgata*.

Key words: Food habit; Long-term study; Snake population; Species diversity loss

Introduction

Long-term field studies have provided evidence of worldwide declines in vertebrate populations, including amphibians and reptiles (e. g., Brashares et al., 2014; Brodie et al., 2021). Some of these cases of population declines can be directly attributed to the factors such as pollution (Harshbarger et al., 2000; Lionetto et al., 2021), habitat loss or change (Feyrer et al., 2007; Huang et al., 2018), disease (LaDeau et al., 2007; Scheele et al., 2019), overexploitation (Whitehead et al., 1997; Chen et al., 2020), invasion of alien species (Lowe et al., 2000; Marshall et al., 2018), and climate change (Reading et al., 2010; Warren et al.,

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2018). Although several studies on lizard and turtle populations have shown that populations have been declining, evidence for decline in snake populations is scarce (Gibbons et al., 2000; Böhm et al., 2013; Saha et al., 2018). Consequently, there is a consensus among herpetologists that more research is needed on snake population dynamics (Seigel and Mullin, 2009). Reading et al. (2010) reported that approximately 17 snake populations (eight species) have declined in Europe, Africa, and Oceania between 1987 and 2009. They identified habitat degradation and a decrease in food resource availability as the likely factors that caused these declines, but clear evidence was not found.

As obligate predators, snakes play an important role in local ecosystems (Arnold, 1978; Beaupre and Douglas, 2009). Their ecological traits, such as body size, activity time, and population fluctuations, are largely influenced by their food resources (Madsen and Shine, 2000; Madsen et al., 2006; Wolfe et al., 2018). Frogs are the major food sources for some snakes and are easily affected by environmental disturbances. Frogs are often used as bioindicators, to assess short-term environmental change (Lindstedt, 2005). In contrast, snake populations are believed to be excellent long-term bioindicators of environmental change (Beaupre and Douglas, 2009). This view can be attributed to the relative stability of home ranges of most snakes over the course of their lifetimes; the ability of snakes to survive in low-energy environments; the use of different habitats during periods of hibernation, foraging, mate searching, and gestation or oviposition; and their low susceptibility to temporary environmental changes (Bauerle et al., 1975; Scott and Seigel, 1992; Beaupre and Douglas, 2009). Therefore, change in a snake population may reflect a major long-term environmental change. However, little is known about the long-term dynamics of snake populations (e.g., Fitch, 2006; Capula et al., 2016; Storniolo et al., 2019).

In Japan, several studies have been conducted regarding seasonal change in snake populations in relation to food resources (e.g., Moriguchi and Naito, 1982; Kadowaki, 1992; Tanaka and Ota, 2002; Hirai, 2004; Mori and Nagata, 2016). However, only one study, Fukada (1992), is available as a long-term study in mainland Japan. Fukada (1992) conducted the study for 16 years, until it was terminated due to industrialization of the survey area. The second-longest survey was conducted by Kadowaki (1996) over a 5-year period, and the environment of that study area has not changed substantially since his study (Fig. 1). In the present study we investigated snake species composition and food habits at the same study site as Kadowaki (1996), which was conducted approximately 30 years ago, and compared our data with those obtained in the previous study.

Materials and Methods

Study site

A field survey was conducted in the rice paddy field (approximately 53.4 ha) at the foot of Hokyo-San Mountain in Tsukuba City (36°09'16" N, 140°07'22" E), located in the center of the main island of Japan, Honshu. The southern side of the area is bordered by paved roads, and the eastern, western, and northern sides are surrounded by secondary forests dominated by sawtooth oak (*Quercus acutissima*), konara oak (*Quercus serrata*), and Japanese red pine, (*Pinus densiflora*) (Fig. 1). The survey area mainly consisted of rice paddy fields, with smaller areas of cultivated land, poultry farms, grasslands, ponds, and streams.

Field survey

The field surveys were conducted twice a week from April to November (spring to autumn) in 2019 and 2020. In total, 113 surveys were made, during the daytime on sunny or cloudy days. Each survey took approximately 4 hours.

Any snake encountered was captured by hand, and the date and time were recorded. Species and sex of the captured snakes were noted. They were measured for snout-vent

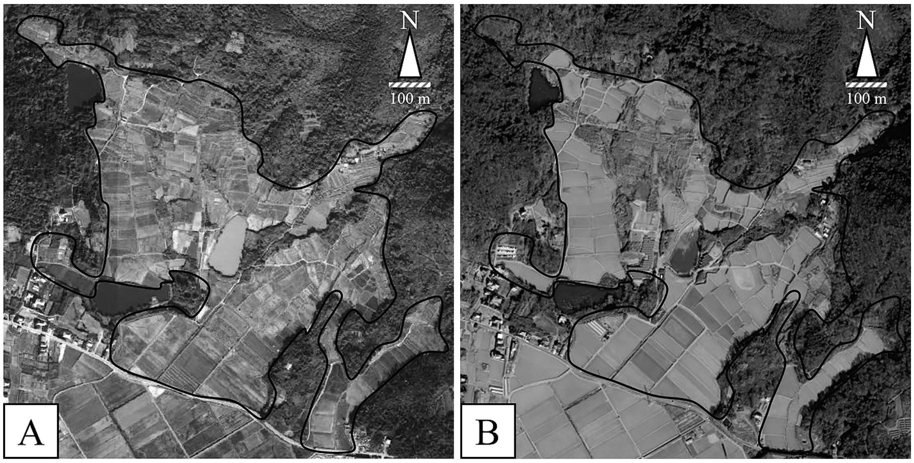

FIG. 1. Satellite maps of the study site around (A) 1990 and (B) 2020.
Study area is surrounded by the black line. The sources of the maps are (A) Geospatial Information Authority of Japan (https://maps.gsi.go.jp/help/intro/looklist/2-nendai.html) and (B) OpenStreetMap (https://www.openstreetmap.org/edit#map=16/36.1538/140.1243). The contrast of the map in panel (A) has been slightly increased from the original to facilitate comparison.

length (SVL), to the nearest 1 mm, and body mass (BM), to the nearest 1 g, and they were forced to regurgitate for the examination of any stomach contents. Finally, snakes were individually marked by clipping subcaudal scales (Blanchard and Finster, 1933) and released at their capture sites.

The regurgitated food items were identified to the species level, whenever possible. The identified food items were classified into two categories: food type (e.g., mammals, lizards, and frogs) and species. In principle, one prey item in the stomach content from a snake was counted as one predation case. However, tadpoles and froglets immediately after metamorphosis found from a single stomach content were treated as a single predation case, because they had likely been concentrated at one spot and could be regarded as a single mass of food.

Statistical analysis

We applied Fisher's exact test for the comparison of snake species composition and food items between the data obtained in the present study and those in Kadowaki (1996). Similarly, a t-test was used to compare SVL and BM between our new data and the previous data (Kadowaki, 1996). The statistical error rate was set at P=0.05. The body condition index (=BM/SVL^3) of each snake and the proportion of snakes containing food items for each species were calculated. R Studio Desktop 1.3.1093 (for Windows 10/8/7) was used for the statistical analyses.

RESULTS

Species composition

Five snake species were recorded during the study period, namely *Rhabdophis tigrinus* (53.0%, n=122), *Gloydius blomhoffii* (26.5%, n=61), *Elaphe climacophora* (12.6%, n=29), *Hebius vibakari* (7.4%, n=17), and *Lycodon orientalis* (0.4%, n=1) (Table 1). The number of snakes captured, including recaptures, was 184, 85, 45, 19, and 2 for *R. tigrinus*, *G. blomhoffii*, *E. climacophora*, *H. vibakari*, and *L. orientalis*, respectively. Compared with Kadowaki (1996), the species composition was significantly different (P<0.01). In particular, no *E. quadrivirgata* were observed in the present study. Similarly, *Euprepiophis conspicillatus*, reported in Kadowaki (1996), was not observed in the present study. *Lycodon orienta-*

TABLE 1. Species composition of snakes in the 1988–1992 and 2019–2020 studies. n: number of captured individuals, excluding recaptures. The data of 1988–1992 are from Kadowaki (1996). Numerals in parentheses indicate the average number of snakes (excluding recaptures) captured per census.

Species	1988–1992		2019–2020	
	n	Frequency (%)	n	Frequency (%)
Rhabdophis tigrinus	184 (0.684)	42.6	122 (1.080)	53.0
Elaphe quadrivirgata	148 (0.550)	34.3	0 (0)	0.0
Gloydius blomhoffii	59 (0.219)	13.7	61 (0.540)	26.5
Elaphe climacophora	27 (0.100)	6.3	29 (0.257)	12.6
Euprepiophis conspicillata	10 (0.037)	2.3	0 (0)	0.0
Hebius vibakari	4 (0.015)	0.9	17 (0.150)	7.4
Lycodon orientalis	0 (0)	0.0	1 (0.009)	0.4
Total	432 (1.606)	100.0	230 (2.035)	100.0

TABLE 2. Comparison of snout-vent length (SVL), body mass (BM), and body condition index of *Rhabdophis tigrinus* and *Gloydius blomhoffii* between the two study periods (1988–1992 and 2019–2020). The data for 1988–1992 are from Kadowaki (1996). *P<0.05.

Variables	Species	Sex	1988–1992		2019–2020		t	df	P
			n	Mean±SD	n	Mean±SD			
SVL (mm)	*R. tigrinus*	Male	80	563±99	53	536±145	1.187	83.9	0.238
		Female	101	656±148	71	649±157	0.284	145	0.777
	G. blomhoffii	Male	60	412±53	25	423±48	–1.018	37.1	0.315
		Female	50	462±29	34	437±60	2.214	45.7	0.032*
BM (g)	*R. tigrinus*	Male	81	65.9±25.8	53	60.2±44.5	0.836	75.1	0.406
		Female	104	119.0±90.0	71	112.5±69.6	0.537	170.3	0.592
	G. blomhoffii	Male	10	46.1±17.0	24	51.8±14.7	–0.989	16.2	0.337
		Female	49	82.1±22.7	34	64.6±25.3	3.209	65.3	0.002*
Body condition index*	*R. tigrinus*	Both sexes	263	0.036±0.008	122	0.036±0.010			
	G. blomhoffii	Both sexes	60	0.079±0.016	61	0.070±0.013			

* Statistical analysis for body condition index was not performed since Kadowaki (1996) only showed mean±SD.

lis, which was not observed in the previous study, was found during the present survey; one individual of this species was found at 1140 h on 15 May 2019 and at 1130 h on 20 May 2019, both times under a metal sheet.

Ecological characteristics of snake species

SVL was not significantly different in *R. tigrinus* for both sexes between the present and 1988–1992 studies (males: t=1.187, df=83.9, P=0.238; females: t=0.284, df=145.0, P=0.777; Table 2). For *G. blomhoffii*, SVL of males did not differ significantly between the studies (t=1.018, df=37.1, P=0.315; Table 2), whereas females showed significant differences (t=2.214, df=45.7, P=0.032; Table 2). BM did not differ significantly in *R. tigrinus* for both sexes between the studies (males: t=0.836, df=75.1, P=0.406; females: t=0.537, df=170.3, P=0.592; Table 2). For *G. blomhoffii*, BM of

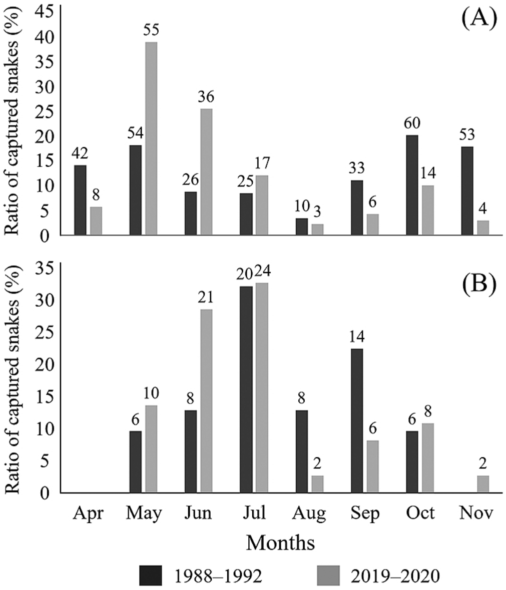

FIG. 2. Seasonal changes in the occurrence of (A) *Rhabdophis tigrinus* and (B) *Gloydius blomhoffii* in 1988–1992 and 2019–2020. Ratio of captured snakes indicates the percentage of snakes captured by month, with the entire year comprising 100%. Numerals above bars are the number of captured snakes, including recaptures. The data of 1988–1992 are from Kadowaki (1996).

males did not differ significantly between the studies (t=0.989, df=16.2, P=0.337; Table 2), whereas females showed significant differences (t=3.209, df=65.3, P=0.002; Table 2). Mean body condition indices of *R. tigrinus* and *G. blomhoffii* were 0.036 and 0.079 in the 1988–1992 study and 0.036 and 0.070 in the present study, respectively (Table 2).

In each year, *R. tigrinus* was observed for the first time between the end of March and the beginning of April in the 1988–1992 study, whereas that species was first sighted on 29 April 2019 and 16 April 2020 in the present study. No clear difference was observed in the first day of sighting of *G. blomhoffii* between the two studies. The seasonal activity pattern of *R. tigrinus* showed a large peak in May and small peak in October, although there had been a large peak in both May and October in the previous study (Fig. 2A). The seasonal activity pattern of *G. blomhoffii* showed a large peak in July and small peak in October in the present study (Fig. 2B).

In *R. tigrinus* there was no significant difference in the proportion of food-type categories in the stomach contents between the 1988–1992 and 2019–2020 studies (P=0.099; Table 3). The difference also was not significant in *G. blomhoffii* (P=0.22; Table 3). However, there were significant differences in the composition of frog species between the present and 1988–1992 studies, both in *R. tigrinus* (P<0.001) and *G. blomhoffii* (P=0.037). In the previous study *R. tigrinus* fed on *Dryophytes japonicus*, *Rana japonica*, and *Pelophylax porosus porosus*, but of these species only *D. japonicus* was found in stomach contents in the present study (Table 3). Furthermore, *Lithobates catesbeianus*, an invasive alien frog species, was observed in the stomach contents of both *R. tigrinus* and *G. blomhoffii* in the present study (Table 3). In both *R. tigrinus* and *G. blomhoffii*, the proportion of snakes that contained food in their stomachs decreased to approximately 10%, compared to about 20–25% in the previous study (Table 4).

DISCUSSION

Our results showed a remarkable decline in *E. quadrivirgata*, which had been one of the dominant species at the study site 30 years ago, whereas *R. tigrinus* and *G. blomhoffii*, which had also dominant at the site 30 years ago, did not show such a decline. *Elaphe quadrivirgata* is known to be a dietary generalist predator on vertebrates (Hasegawa and Moriguchi, 1989; Fukada, 1992; Kadowaki, 1992; Tanaka and Ota, 2002). Although many studies have reported that *E. quadrivirgata* feeds mainly on frogs (e.g., Fukada, 1992; Kadowaki, 1992), several studies have shown that the snake feeds on lizards as its main food in island environments (e.g., Hasegawa and Moriguchi, 1989; Tanaka and Ota, 2002). Theory predicts that generalists are more resistant to environmental changes than specialists, and empirical studies have supported this prediction (Angermeier,

TABLE 3. Food habits of *Rhabdophis tigrinus* and *Gloydius blomhoffii* in 1988–1992 and 2019–2020. The number of individual prey items is shown, except for tadpoles and metamorphosed froglets, for which the number of snakes that contained those prey items is counted. The data of 1988–1992 are from Kadowaki (1996).

Food type	Frog species	*R. tigrinus*		*G. blomhoffii*	
		1988–1992	2019–2020	1988–1992	2019–2020
Frog	*Dryophytes japonicus*	48	22	0	0
	Rana japonica	32	0	4	1
	Pelophylax porosus porosus	31	0	2	0
	Zhangixalus schlegelii	3	1	0	0
	Bufo japonicus	2	1	0	0
	Lithobates catesbeianus	0	2	0	1
	Unidentified tadpoles	0	1	0	3
Mammal	—	0	0	4	1
Lizard	—	0	0	0	2
Snake	—	0	0	1	1
Fish	—	1	2	3	0
Total		117	29	14	9

TABLE 4. The proportion of snakes that contained food in their stomachs. The data for 1988–1992 are from S. Kadowaki (personal communication).

Species	1988–1992		2019–2020	
	n	Frequency (%)	n	Frequency (%)
Rhabdophis tigrinus	263	25.30	122	11.41
Gloydius blomhoffii	60	20.97	61	10.59

1995; Terraube et al., 2011). However, our finding of the decline in a dietary generalist contradicts this theoretical prediction. On the other hand, many studies have reported declines in an entire snake community, including communities that consist of a single species (e.g., Santos and Llorente, 2009; Li et al., 2013; Graitson et al., 2019; Tolley et al., 2019). Only a few studies have shown a decline limited to a certain species in a larger snake community (e.g., Croshaw et al., 2019; Storniolo et al., 2019). Considering that large-scale disturbances, such as overhunting and urbanization, which can have catastrophic direct impacts on a snake community, did not occur at the present study site, it is possible that the decline of a single species of snake is a consequence of other factors, which are currently unknown.

Compared to the previous study (Kadowaki, 1996), *R. tigrinus*, which is known as an anuran-eater (Fukada, 1992; Kadowaki, 1992; Hirai, 2004; Mori and Nagata, 2016), showed a marked bias in the frog species composition in its diet, and a decrease in the proportion of snakes with stomach contents was observed. *Gloydius blomhoffii*, which is known as a dietary generalist that consumes frogs, reptiles, and mammals (Hamanaka et al., 2014; Mori, 2021), also showed a decrease in the proportion of snakes with stomach contents. In addition, both *R. tigrinus* and *G. blomhoffii* contained *L. catesbeianus*, an exotic frog species, in their diets. These results may imply that the species diversity of native frogs and abundance of food resources (frogs, reptiles, and small mammals) that were previously exploited by *R. tigrinus* and *G. blomhoffii* have decreased since the time when the previous study was conducted.

In the present study, the stomach contents of *R. tigrinus* were dominated by *D. japonicus* at 75.9%, whereas *R. japonica* and *P. porosus* were not detected. This prey composition may reflect the seasonal activity pattern of the snakes observed in the present study: high in May and June and low in October, compared to the previous study of 1988–1992. In general, snake activity pattern is strongly influenced by food resources (Madsen and Shine, 2000; Madsen et al., 2006, Wolfe et al., 2018). To evaluate the relationship between the activity pattern of *R. tigrinus* and its anuran prey, a further survey of seasonal prey abundance is needed.

In summary, our study showed that *E. quadrivirgata* had drastically decreased over approximately 30 years. This snake is a dietary generalist, feeding on frogs, lizards, birds, and small mammals. On the other hand, two other dominant species, *R. tigrinus* and *G. blomhoffii*, 30 years ago are still dominant in the present study. *Rhabdophis tigrinus* depends mostly on frogs as food resources, and *G. blomhoffii* is a generalist, as is *E. quadrivirgata*. The change in the guild structure of frogs might be one of the factors that has affected the guild structure of snakes in the study area. In any event, our study provides a unique case of a decline of a generalist predator in the snake community.

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