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Food Habits of the Taiwan Beauty Snake, *Elaphe taeniura friesi*, as an Introduced Species on Okinawajima Island

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Abstract: The Taiwan beauty snake, *Elaphe taeniura friesi*, has established a stable population in the central part of Okinawajima Island, and there are concerns about the negative effects of the snakes' predation on the native fauna. Thus, we examined the stomachs of 239 *E. t. friesi* specimens collected on Okinawajima Island from July 2018 to November 2019. Stomach contents were identified to the species level whenever possible based on morphological observations and/or DNA analyses. Of the 239 snake specimens, 39 (12 males, 16 females, and 11 juveniles) had contents in their stomach, including 67 prey items, 75% of which were mammals (Muridae and Soricidae) and the rest of which were birds (Pycnonotidae, Cisticolidae, and Columbidae). *Rattus rattus* occurred most frequently; 25 of the 39 snakes examined had this species in their stomachs. All avian prey items detected were nestlings and eggs. Twelve snakes had multiple prey items in their stomach, including in most cases either nestlings of passerine birds or infants or subadults of *R. rattus*. Therefore, *E. t. friesi* is an endotherm consumer that occasionally preys on nestlings and infant rats. These food habits suggested that *E. t. friesi* uses various habitats, from the humus layer on the ground to the branches of trees, for foraging. Several endangered endemic rodent and bird species exist in the northern area of

Okinawajima Island; thus, our results provide a warning about potential negative impact on such animals when *E. t. friesi* expands its range to the northern part of the island.

Key words: Invasive alien species; Diet; DNA barcoding; Morphology; Prey identification

Introduction

Elaphe taeniura is a large terrestrial to semi-arboreal snake that can grow to a length >2 m. This species is widely distributed from the southern part of the Ryukyu Archipelago, Japan, through Taiwan, eastern and southern China, to Southeast Asian countries including Borneo and Sumatra, Indonesia, the southernmost extent of the distribution range (Uetz et al., 2021). Several subspecies of *E. taeniura* are known. In Japan, the endemic subspecies *Elaphe taeniura schmackeri* is found on the Yaeyama and Miyako Islands in the southern part of the Ryukyus and has been listed as Vulnerable in the Japanese Red List (Ministry of the Environment of Japan, 2020). *Elaphe taeniura friesi*, another *E. taeniura* subspecies endemic to Taiwan, is also a threatened species and is protected by national law in Taiwan (Council of Agriculture in Taiwan under Executive Yuan, 2019). Around the end of the 1970s, this Taiwanese subspecies was found in the central part of Okinawajima Island, an island of the central Ryukyus, where no indigenous population of *E. taeniura* ssp. occurs (Nishimura, 2002), and it was considered to have established a population at least before the late 1980s (Katsuren et al., 1996; Ota, 1999). During the 1970s to 1980s, many *E. t. friesi* individuals were imported from Taiwan for display in tourist facilities on Okinawajima Island, and the deliberate release or involuntary escape of some captive snakes is considered the source of the established population (Nishimura, 2002; Japan Wildlife Research Center, 2019).

Elaphe taeniura friesi is currently designated as an invasive alien species under the Invasive Alien Species Act in Japan, along with *Protobothrops mucrosquamatus*, which was also introduced from Taiwan via a similar process (Ministry of the Environment of Japan, 2021). There are concerns that these snake species may have negative effects on endemic species through their predation activity, especially if they expand their range to the northern, mountainous region of Okinawajima Island. Therefore, the Ministry of the Environment of Japan and the Nature Conservation Division of the Okinawa Prefectural Government have implemented measures to survey and control the established populations of these snake species, including the use of snake trapping and purchasing *E. t. friesi* individuals from local people (Japan Wildlife Research Center, 2019).

Predation is a common negative effect of alien species on native ecosystems. Compared with the effects of invasive predator introductions to continents, such introductions into island ecosystems may affect native species, including endemic species, more severely (Reaser et al., 2007; Russell et al., 2017). Because there are no congeneric native snakes on Okinawajima Island and various endangered endemic small animals exist on the island, the establishment of an *E. t. friesi* population is a serious concern in terms of native ecosystem conservation (Nishimura, 2002; Japan Wildlife Research Center, 2019). Although a few studies have found that *E. t. friesi* feeds on mammals (e.g., *Rattus rattus* and Soricidae), birds, and frogs (Lee and Lue, 1996; Shang et al., 2009), a detailed study on the food habit of this subspecies has yet to be conducted on Okinawajima Island or in Taiwan (Mori and Moriguchi, 1988; Hamanaka et al.,

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2014). In the present study, we examined the stomach contents of *E. t. friesi* specimens captured on Okinawajima Island to determine its food habits, including its dietary repertoire, and seasonal and ontogenetic changes in diet. Based on our results, we discuss the potential impact of this invasive predator on the native fauna of Okinawajima Island.

Materials and Methods

Sampling

In total, 239 *E. t. friesi* individuals were collected from July 2018 to November 2019: 219 were captured by local people and local governments, 15 were accidentally captured in traps set for the viperid snake, *Protobothrops flavoviridis*, and the remaining five were captured in traps set for *E. t. friesi*. The collection locations of these 239 snakes were spread across the central part of Okinawajima Island, including Uruma City, Okinawa City, Onna Village, Yomitan Village, Kin Town, Kadena Town, Chatan Town, and Nago City (Fig. 1). All snake specimens were stored in a frozen state until they were used.

Before examinations, the frozen specimens were allowed to defrost. Their snout-vent length (SVL) was then measured to the nearest 1 mm using a tape measure, and their sex was determined using a sex probe for snakes or by examining the external shape of the tail base. Based on observations in captivity, *E. t. friesi* attains sexual maturity when the SVL is 120 cm in females and 105 cm in males (Kamura and Nishimura, 1999); therefore, in the present study, snakes with smaller SVL values were treated as juveniles. By dissecting specimens, they were checked for the presence or absence of stomach contents, and the contents (if any) were removed from the stomach. The stomach contents were preserved in 70% ethanol and tissues used for DNA analysis were in 99% ethanol.

Analysis of stomach contents

Prey items collected from the snakes' stomachs were examined, and species (where possible) and life stage were identified. Observations were conducted with the naked eye or under a stereomicroscope. In general, snakes swallow their prey whole; thus, identifying the species by observation of external morphology and counting the number of the prey items in the stomach are usually not difficult, unless prey have been heavily digested. When mammalian items had been heavily digested, or only small body parts were retrieved, we examined the morphological features of hairs under a stereomicroscope or an optical microscope to identify taxa according to the method of Asato and Izawa (2020). When an item could not be identified at the species level, the family level was used instead.

It was often difficult to identify the species for birds found in the stomachs based on morphological features because most bird prey items were nestlings or eggs. Therefore, we conducted DNA analysis on the avian samples.

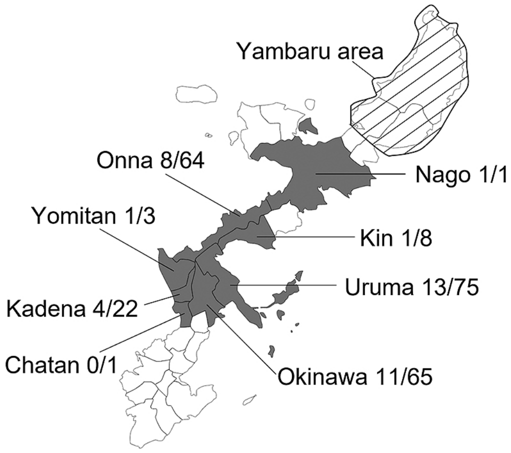

Fig. 1. A map of Okinawajima Island showing sampling location of *Elaphe taeniura friesi* specimens examined. Gray areas indicate the municipalities where the samples of *E. t. friesi* individuals were collected, and hatched area indicates the Yambaru Area, where many endemic endangered animals and plants occur but no *E. t. friesi* was recorded up to now. Numbers denoted after location names indicate the number of snakes with stomach contents/the total number of snakes collected in each location.

Total DNA was extracted from a piece of liver tissue of the nestlings and the eggshell membrane using a DNeasy Blood & Tissue Kit (Qiagen) following the manufacturer's instructions. The DNA barcoding region of mitochondrial cytochrome c oxidase I (CO1) was amplified using standard polymerase chain reaction (PCR) following the method of Saitoh et al. (2015). The PCR primers used in this study were as follows: BirdF1 (5'-TTCTCCAA CCACAAAGACATTGGC-3') and BirdR1 (5'-ACGTGGGAGATAATTCCAAATCCTG-3') or L6697Bird (5'-TCAACYAACCACAAAGAY ATCGGYAC-3') and H7390Thrush (5'-ACGT GGGARATRATTCCAAATCCTG-3'). After verifying amplification using 1% agarose gel electrophoresis, the PCR product was purified with PEG precipitation. The purified PCR product was subjected to a cycle sequencing reaction using a BigDye v3.1 Kit (Applied Biosystems) and the following cycling conditions: 96°C for 1 min and 25 cycles at 96°C for 10 s, 50°C for 5 s, and 60°C for 4 min. After further purification via ethanol precipitation, the reaction products were subjected to sequencing, which was conducted by Macrogen Japan Corporation (Tokyo). For species identification, the obtained sequences were used in a nucleotide homology search via BLAST in the DNA Data Bank of Japan. Avian samples for which DNA sequences could not be obtained were recorded simply as "bird." Parasites and plant pieces detected in the stomachs were excluded from the analysis. To evaluate the relative importance of prey species, the frequency of occurrence (FO, i.e., (the number of snakes with a particular prey item in their stomach/the total number of snakes examined) ×100) was calculated for each prey species.

Results

In the adult-sized *E. t. friesi* examined in this study, there was no significant difference in SVL between males (n=80) and females (n=72) (Wilcoxon rank sum test, P=0.12). Of the 239 snakes examined, 39 (12 males, 16 females, and 11 juveniles) had prey items in their stomach (16.3% of all snakes), and 67 prey items were obtained. The mean SVL of the snakes with stomach contents was 130.9±14.5 cm (112.1–163.5 cm) [mean±SD (range)] for males, 146.9±13.2 cm (123.8–172.6 cm) for females, and 79.0±25.9 cm (39.6–112.2 cm) for juveniles. The mean SVL of the snakes without stomach contents was 140.2±19.4 cm (106.2–191.2 cm) for males, 140.6±13.2 cm (122.0–172.1 cm) for females, and 76.5±29.3 cm (31.5–118.0 cm) for juveniles. There was no significant difference in SVL between snakes with and without stomach contents in all three sex-age categories (Wilcoxon rank sum test, males: P=0.10, females: P=0.09, Juveniles: P=0.64).

The obtained prey items were either mammals or birds (including eggs) (Table 1). Mammals occurred most frequently (FO=92.3%) followed by birds (17.9%). Four mammalian species and three avian species were identified to the species level. *Rattus rattus*, found in 25 of 39 snake stomachs (64.1%), was the most frequently detected prey species, followed by *Suncus murinus* (10.3%), *Crocidura watasei* (5.1%), and *Mus caroli* (2.6%) among the mammalian species. In addition, one Muridae individual and three Soricidae individuals were found in the stomachs of four snakes, but these prey items could not be identified to the species level because even their hairs were considerably digested. Of the avian prey species, *Pycnonotus sinensis* (5.1%), *Cisticola juncidis* (5.1%), and *Streptopelia orientalis* (2.6%) were identified with 99–100% sequence identity relative to many of their respective references. Two other avian prey items were eggshells and feathers, but the species of these could not be identified owing to failure in PCR amplification or DNA sequencing. Among the avian items that could be identified to the species level, one was a clump of crushed *P. sinensis* eggshell and all others were nestlings.

The stomach contents were obtained from April to November during the 2018 and 2019 sampling periods, for which snake samples were available. Mammalian prey items were

TABLE 1. Prey items detected in the stomachs of *Elaphe taeniura friesi* captured on Okinawajima Island. The numbers of snakes that had consumed the listed prey taxa are shown followed by the frequency of occurrence (%) in parentheses.

Taxon			Male (n=12)	Female (n=16)	Juvenile (n=11)	Total (n=39)
Mammal						36 (92.3)
	Rodentia	*Rattus rattus*	10 (83.3)	10 (62.5)	5 (45.5)	25 (64.1)
		Mus caroli	0	1 (6.3)	0	1 (2.6)
		Unidentified Muridae	0	1 (6.3)	0	1 (2.6)
	Eulipotyphla	*Suncus murinus*	1 (8.3)	3 (18.8)	0	4 (10.3)
		Crocidura watasei	0	0	2 (18.2)	2 (5.1)
		Unidentified Soricidae	0	0	3 (27.3)	3 (7.7)
Aves						7 (17.9)
	Passeriformes	*Pycnonotus sinensis*	0	1 (6.3)	1 (9.1)	2 (5.1)
		Cisticola juncidis	0	0	2 (18.2)	2 (5.1)
	Columbiformes	*Streptopelia orientalis*	0	1 (6.3)	0	1 (2.6)
		Unidentified bird	1 (8.3)	0	1 (9.1)	2 (5.1)

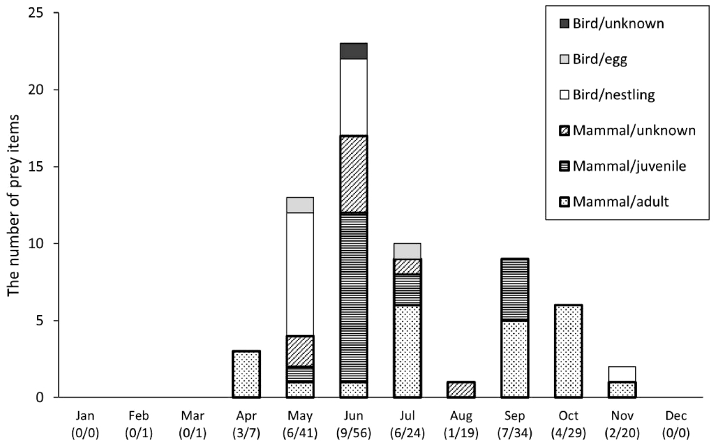

FIG. 2. Seasonal changes in the diet of *Elaphe taeniura friesi*. Prey types are assigned to the six categories according to animal group and life stage. "Mammal/juvenile" includes both subadults and infants. Where the life stage of the prey items was "unknown," only hairs, feathers, and/or bones were retrieved from the stomach of the predator. Numbers in parentheses under the months indicate the number of snakes with the stomach contents/the total number of snakes. Of the 239 snake specimens, seven did not known the month they were captured.

detected in the stomachs in all of these months, whereas avian prey items were only detected in May–July and November (Fig. 2). Among the avian prey species, eggs were detected in May and July (from *P. sinensis* and an unidentified bird), whereas nestlings were detected in May–July (*C. juncidis* and *P. sinensis*) and November (*S. orientalis*).

The mean number of prey items found in a single stomach was 1.71±1.63. Twelve snakes had multiple prey items in their stomach, with nine items being the maximum (Table 2; No. 30). In two cases, multiple adult-sized *S. murinus* were found in a single snake. *Rattus rattus*

TABLE 2. Composition of the stomach contents of 12 *Elaphe taeniura friesi* individuals that had consumed multiple prey items. The number of prey items is shown for various taxa. Rr: *Rattus rattus*; UM: unidentified Muridae; Sm: *Suncus murinus*; Cw: *Crocidura watasei*; US: unidentified Soricidae, Ps: *Pycnonotus sinensis*; Cj: *Cisticola juncidis*.

	Sampling date (yr. mo)	Snake sex	Prey taxon	Lifestage of prey items			
				adult	subadult	hatchling/infant	other
No. 3	2018.9	J	Cw+US	2			
No. 4	2018.9	M	Rr			2	
No. 12	2018.10	F	Sm	2			
No. 13	2018.10	F	UM	2			
No. 22	2019.5	J	Ps			4	
No. 28	2019.6	F	Rr		2		
No. 36	2019.6	M	Rr	1		5	
No. 38	2019.7	M	Rr		2		
No. 42	2019.7	M	Sm	3			
No. 21	2019.5	J	US				1 (only hair)
			Cj			4	
No. 30	2019.6	F	Rr		4		
			Ps			5	
No. 39	2019.7	F	Rr	1			
			Ps				1 (egg)

was the only species for which infants or subadults were found in the snakes' stomachs, and five of eight snakes that contained *R. rattus* infants or subadults had multiple individuals in their stomachs. One of these snakes had eaten one adult female and five infants (Table 2; No. 36). According to the positions of these rats in the snake's stomach, the adult female was likely swallowed first followed by the infants. For bird species other than *S. orientalis*, multiple nestlings were found in the same snake stomach. Although each snake stomach mostly contained single prey species, three stomachs contained both mammals and birds simultaneously, and one stomach contained four *R. rattus* infants and five *C. juncidis* nestlings (Table 2; No. 30).

Muridae was detected in the stomachs of relatively large (SVL>80 cm) *E. t. friesi* individuals (Fig. 3). However, even in large snakes, small prey items, such as infants or subadults of *R. rattus*, were also detected. Two soricid species tended to be found in either large or small *E. t. friesi* individuals: *S. murinus* in large snakes (SVL=120–160 cm) and *C. watasei* and several small unidentified Soricidae in small snakes (SVL<90 cm and mostly <50 cm) (Fig. 3). Birds were detected in the stomachs of snakes with a wide range of SVLs.

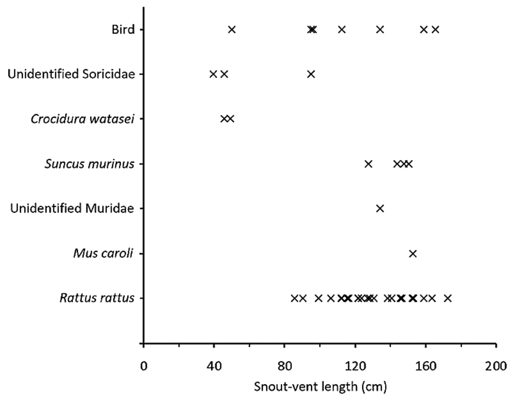

FIG. 3. Relationship between the snout-vent length of *Elaphe taeniura friesi* and the prey taxa found in their stomach.

Discussion

Our results suggest that the introduced *E. t. friesi* on Okinawajima Island exclusively prey on mammals and birds. This finding is largely consistent with previously reported results, i.e., regarding the diet of this subspecies in Taiwan; however, we did not detect any frogs in the snakes' stomachs, despite frogs having been reported as one of the main *E. t. friesi* prey items in Taiwan (Lee and Lue, 1996; Shang et al., 2009) and being abundant in central part of Okinawajima Island. Previous studies (Takara, 1963; Ota, 2014; Asato et al., 2021) have found that *E. t. schmackeri* (the southern Ryukyu subspecies) also preys on mammals and birds. Among the *E. t. schmackeri* prey species of previously reported, *R. rattus*, *M. caroli*, and *C. juncidis* were also detected in the present study. Thus, *E. taeniura* ssp. are primarily endotherm consumers, and the population of *E. t. friesi* on Okinawajima Island also has this food habit.

The FO of mammals in the present study was >90%. In particular, *R. rattus* was found most frequently in all survey months, indicating that it is the most common prey species for *E. t. friesi* on Okinawajima Island. Our *E. t. friesi* samples were caught in villages, cultivated fields, and woodland, indicating that this species occurs in a wide range of habitats. *Rattus rattus* is a common invasive alien species on Okinawajima Island, and it also appears in various habitats, e.g., close to villages and in semi-natural forests (Iwasa, 2015). Therefore, this rat species is likely to be frequently encountered by *E. t. friesi*.

The FO of birds in the present study, 17.9%, was lower than that of mammals. Avian prey items were found during a limited period from May to July, except for a single case of *S. orientalis* in November. As far as we could identify, all avian prey items were nestlings or eggs. In general, May–July is the breeding season for passerine birds, and both *C. juncidis* and *P. sinensis* breeding has been observed during this period on Okinawajima Island (Kinjo, 1993; Yonashiro, 1999). Nakamura and Sameshima (2012) reported that *S. orientalis* sometimes breeds in the winter, and the oviposition of this species has been detected in October on Okinoerabu Island near Okinawajima Island. Thus, *E. t. friesi* on Okinawajima Island apparently targets eggs and nestlings rather than adult birds, chiefly in spring to early summer. The absence of adult birds in the stomach contents of *E. t. friesi* may imply that it attacks bird nests exclusively during daytime, consistent with this species being diurnal (Shang et al., 2009). However, since DeGregorio et al. (2015) demonstrated that a primary diurnal but facultatively nocturnal western rat snake, *P. obsolata*, rarely captured adult birds in bird nests even during the night, and thus, this issue needs to be clarified by additional investigation.

Pycnonotus sinensis and *S. orientalis* nest in trees (Murakami and Fujimaki, 1983; Kinjo, 1993). *Elaphe taeniura friesi* in Taiwan has also been observed feeding on hatchlings in a nest in the top of a 7 m-tall tree (Shang et al., 2009). In central China, *E. t. taeniura* is one of the major predators of eggs and nestlings of *Accipiter soloensis*, which nests in trees (Ma et al., 2016). In contrast, the soricid shrews as other prey taxa of *E. t. friesi* on Okinawajima Island are strictly ground-dwellers, with their main habitats comprising the thick litter and humus layers formed on the ground (Abe, 1994). Therefore, the dietary repertoire of *E. t. friesi* indicates that this species uses both terrestrial and arboreal habitats for foraging.

Many species of snakes are known to change their food habits with growth (Lillywhite, 2014). In the present study, smaller snakes preyed on smaller Soricidae, whereas *R. rattus*, a relatively large prey species among the dietary repertoire of *E. t. friesi*, was found only in the stomachs of larger snakes (SVL>80 cm), even though this rat species was found in the >70% of stomachs of large snakes (Fig. 3). Thus, *E. t. friesi* on Okinawajima Island seem to shift their diets with growth to some extent. Nevertheless, larger snakes ate not only large but also small prey, such as *R. rattus* juveniles and nestlings of small passerine birds. This pattern corresponds to the "ontogenetic telescope," which is relatively common in snakes (Rodríguez-Robles, 2002).

Colonization of a snake species on an island sometimes has severe negative effects on the native fauna. A famous example is the case of *Boiga irregularis* introduction to Guam; the introduced species caused the extinctions of a considerable number of native small animals, including rodents, bats, land birds, sea birds, and lizards (Savidge, 1987; Rodda et al., 1997; Fritts and Rodda, 1998). The present results show that *E. t. friesi* preys on *C. watasei*, which is endemic to the central Ryukyu Islands and listed as Near Threatened in the Japanese Red List (Ministry of the Environment of Japan, 2020). The distribution range of *E. t. friesi* on Okinawajima Island is currently restricted to the central part of the island where most areas have more or less affected by anthropogenic disturbance, so that not many Okinawan endemic endangered species occur. However, *E. t. friesi* is certainly expanding its range, especially to the north (Nature Conservation Division of the Okinawa Prefectural Government, 2020), and its northern area includes mountainous natural forests, the so-called Yambaru Area (Fig. 1), which is registered as a World Natural Heritage Site and contains many endemic endangered animals and plants. Indeed, several Yambaru endemic small mammals and birds, such as the Okinawa spiny rat *Tokudaia muenninki* and the Ryukyu robin *Luscinia komadori namiyei*, are highly threatened. Given that *E. t. friesi* preys on rats and passerine birds, we would expect that further northward expansion of its distribution on Okinawajima Island will have negative effects on these threatened animals. To avoid the worst scenario and conserve irreplaceable ecosystems in Yambaru, further countermeasures to control the *E. t. friesi* population on Okinawajima Island are urgently required.

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