Feeding Characteristics of a Japanese Pitviper, *Ovophis okinavensis*, on Okinawa Island: Seasonally Biased but Ontogenetically Stable Exploitation on Small Frogs

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Abstract: *Ovophis okinavensis* is an endemic pitviper of the subtropical region of Japan. Based on information from various localities, the species has been considered a dietary generalist that exploits various terrestrial vertebrates. We analyzed stomach contents of *O. okinavensis* in a northern mountain area on Okinawa Island, based on data of a 10-years-study, to examine its trophic features at the population level. We recovered a total of 461 prey items, which were comprised of six, three, five, and three species of frogs, reptiles, birds, and mammals, respectively. Approximately 93% of dietary items consisted of frogs, the majority of which belonged to two explosively breeding species aggregating to restricted spots along the stream only during their reproductive season (winter). On the other hand, from April to November, the snake mainly depended on vertebrates other than frogs. Neither an ontogenetic dietary shift nor intersexual dietary divergence was evident although males tended to exploit one of the two explosively breeding frog species more frequently than females. There were weak positive correlations between snake size and prey size, but large snakes did not drop small prey items from their diet. Average body mass of each prey item was only 5.2% of snake body mass. Characteristics of trophic features of *O. okinavensis* of this population, such as extremely high dependency on frogs in winter, the absence of ontogenetic dietary shift, and utilization of small sized prey, are discussed in comparison with other viperids.

Key words: Crotalinae; Prey size; Ontogenetic dietary shift; *Ovophis okinavensis*; Sexual difference

INTRODUCTION

Viperidae is one of the much diversified snake families widely radiating over the world

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exclusive of Australasia and Antarctica (Pough et al., 2004). Since those early works by a few authors, such as Saint Girons (1952), Fitch (1960), and Klauber (1972), the trophic ecology and feeding characteristics of viperid snakes have been relatively well studied chiefly on the basis of data from European and North American species. With respect to members

of the family from other regions, most comparable studies started much more recently (South America: Valdujo et al., 2002; Nogueira et al., 2003; Monteiro et al., 2006, Central Africa: Luiselli and Akani, 2003; Ineich et al., 2006, Southeast Asia: Daltry et al., 1998; Creer et al., 2002; Mori et al., 2002; Shine and Sun, 2003; Lin and Tu, 2008), but these studies also have revealed their diverse feeding habits as ranging from frog specialists (Ineich et al., 2006) to vertebrate generalists (Creer et al., 2002; Valdujo et al., 2002; Monteiro et al., 2006). These studies, as well as several other studies on some North American species, have also highlighted a possible common tendency of ontogenetic dietary shift, typically from ectothermic to endothermic prey (Klauber, 1972; Campbell and Lamar, 1989; Daltry et al., 1998; Shine and Wall, 2007; Lin and Tu, 2008), along with improvement of ability to ingest larger prey through structural modifications of trophic apparatus, an evolutionary innovation characteristic to viperid snakes (Pough and Groves, 1983; Greene, 1992; but see Cundall and Deufel, 2006). Nonetheless, a great majority of the Asian and African viperids remains to be studied (Ineich et al., 2006). Furthermore, dietary information on a given Asian or African species, even when available, mostly derives from museum specimens originated from various localities: very few population-based studies have been conducted despite their obvious importance for our better understanding of feeding traits in an evolutionary framework (Thompson, 2005).

Ovophis okinavensis is a small, subtropical pitviper distributed on islands in the central part of the Ryukyu Archipelago, Japan. Currently available dietary records of wild *O. okinavensis* cover all terrestrial vertebrate classes (Nakachi, 1991; Mori et al., 2002; Toda et al., 2003; Kadota, 2006, 2011; see Mori and Moriguchi, 1988 for other references), implying that this species is a generalist feeder. On the other hand, despite the abundance of dietary records, few studies have examined patterns and causes of variations in feeding characteristics within a single population of *O.*

okinavensis, such as sexual differences, ontogenetic shift, seasonal change, and effects of snake's body size on the prey properties. Here, we investigate the feeding habit of *O. okinavensis* by analyzing sexual, ontogenetic, and seasonal divergences in prey taxa and size, based on a long-term study conducted in the northern mountain area on Okinawa Island. We then discuss the trophic features of this pitviper by comparing its general feeding habits with those of other viperid snakes previously reported.

MATERIALS AND METHODS

The diet of *O. okinavensis* was examined on the basis of the stomach contents of individual snakes captured from December 1996 to February 2006 in a limited area of the northern part of Okinawa Island, Ryukyu Archipelago, Japan. The main study area (ca. 25 ha) encompasses the upper streams of Zatsun River and surrounding hilly environments of Yambaru. Vegetation was dominated by primary and well-recovered secondary forests consisting of humid-subtropical broad-leaved evergreen trees such as *Castanopsis sieboldii*. Meteorological data of the study region is shown in Mori et al. (2002). Field study was made throughout the year but with particular intensities from December to March for the purpose of investigating the relationship of a winter activity of the snake with the breeding activity of two species of frogs, *Rana* sp. (formerly erroneously referred to as *R. okinavana*, see Matsui [2007]; hereafter referred to as *Rana* sp. A) and *R. narina*, both breeding in the stream (Mori et al., 2002, 2009). Basically, we haphazardly walked at night along streams and trails, which run though the study area irregularly, searching for snakes on the surface. Whenever we found individual snakes, we collected them except for the cases specified below. We also searched between rocks, insides of crevices of ledges, and in burrows on banks.

In addition to the above surveys, we also used a road cruising technique to find snakes

on the road to collect dietary data from different habitats. The road is an approximately 7 km segment of the routes Benoki, Ie, and Chinufuku, which partially surrounds the main study area and crosses the Yambaru forests. These routes run through various habitats, such as forests along hill ridges, slopes, and streams, and a forest park with more open habitats. The straight distance from the main study area to the farthest point of the segment is approximately 3 km. The width of the paved road varied from 5 to 8 m. We drove at 20 to 40 km/h, depending on visibility, and collected snakes whenever we found them on the way to and back from the main study area.

Snakes were brought to the nearby field station within 12 hours of collection, where they were measured for snout-vent length (SVL), body mass (BM), maximum head width (MHW), interocular distance (IOD: distance between exterior edges of eyes), and upper jaw length (JL: straight distance between the tip of the snout and the posterior edge of the eighth supralabial). MHW and JL were measured while the snakes were gently held by the neck region so as to keep the head slightly above the substrate and the mouth closed. Although JL is not a direct measurement of the upper jaw, we used this measurement as one of the approximate indices of head size. Sex was determined by using a probe, by everting hemipenes, or by examining the external shape of the tail base. Stomach contents were examined by palpation and forced-regurgitation. Recovered prey items were identified and measured for MHW, SVL, and BM whenever possible. Direction of ingestion of each prey item was determined either as head first, hind (tail or hindleg[s]) first, or midbody first (swallowing by bending at the midbody of the prey). When the prey items were frogs, they were basically fed back to the stomach after identification and measurements. Unidentified items and animals other than frogs were preserved in 10% formalin for later identification and measurements. The snakes captured and examined were individually marked by ventral

scale clipping and by painting numbers on dorsal surfaces of head and posterior body for permanent and temporal visual identifications, respectively. In addition, from August 1998, small (11.5×2.2 mm) passive integrated transponder (PIT) tags were injected under the skin for individual identification. Each snake was released at the site of capture basically within 24 hours after collection.

When we found snakes that had been collected and released within a few weeks before (visually determined by checking the painting), we usually did not collect them or did not examine stomach contents so as not to disturb them too frequently. Prey animals confirmed by direct observations on predation were also recorded as food items.

In our earlier study, only a few snakes were found along the stream by visual census between late spring and late fall (Mori et al., 2002). We therefore periodically examined between March 2004 and February 2005 stomach contents of four radio-tracked snakes (two males and two females), to which we surgically implanted radio tags (Holohil SB-2T, 5 g) intraperitoneally following the procedures described by Reinert and Cundall (1982) and Nishimura et al. (1995). These snakes were initially collected along the stream and released at the site of capture four to six days after surgery. We located the radio-tracked snakes once every two weeks and collected them to examine the presence of the stomach contents unless they stayed away from our access, such as under large rocks or in deep crevices. If the snakes had stomach contents, we processed them in the same way as described above. The original data of stomach contents collected between December 1996 and March 2000 are the same as those presented in Mori et al. (2002).

Sexual differences of SVL and total prey body mass were examined using Welch t-test because of the heterogeneity of variance. Relative head size was compared between the sexes by ANCOVA using log transformed data with SVL as the covariate. Student t-test and ANOVA were used for other comparisons of

means between two groups and among more than two groups, respectively. Differences in diet composition between the sexes and among seasons were examined using Fisher's exact probability test. Correlations of snake size and prey size were examined using Kendall rank correlation. For the analyses of snake body measurements, only the data for each individual at first capture were used so as to ensure the statistical independence of each data set. All statistical analyses were conducted using StatView (ver. 5.0, SAS, Inc., Cary, NC; http://www.statview.com) with a significant level of P=0.05.

RESUTLS

Females were significantly larger in SVL than males (Welch t-test, df=1, 257.16, t=7.21, P<0.0001: female, x̄±SE=481±6.3 mm; male, 430±3.5 mm). ANCOVA revealed significant sexual differences in slope of regression lines between SVL and MHW (df=1, 366, F= 23.71, P<0.0001). Females have relatively wider head than males, and this difference becomes clearer as the body size of snakes becomes larger (Fig. 1A). There were no significant sexual differences in either slope or elevation in regression lines between SVL and IOD (slope, df=1, 366, F=0.41, P=0.847; elevation, df=1, 366, F=0.25, P=0.620) and between SVL and JL (slope, df=1, 366, F= 0.82, P=0.366; elevation, df=1, 366, F=0.41, P=0.525). There were significant sexual differences in slope in regression lines between JL and MHW (df=1, 366, F=40.24, P< 0.0001). Females showed relatively wider and shorter head than males (Fig. 1B).

A total of 461 prey items, consisting of six species of frogs, one species of lizards, two species of snakes, five species of passerine birds, and one species each of rodents, shrews, and bats, were identified (Table 1). Nearly 93% of the prey items were frogs, and the majority (85.9%) of them consisted of two species, *R. narina* and *Rana* sp. A. There were no significant differences in the frequency of frogs in food items between the sexes (frogs
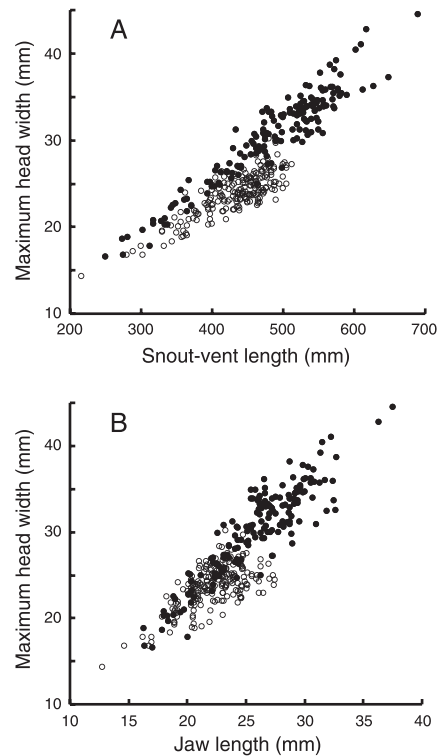

FIG. 1. Comparisons of maximum head width against snout-vent length (A) and jaw length (B) between male (open circles) and female (closed circles) *Ovophis okinavensis*.

vs. other three taxa combined, Fisher test, P=0.173). However, when only those two predominant frog species were considered, males had *Rana* sp. A more frequently than females, and the latter had *R. narina* more frequently than the former (P<0.0001).

In January-March approximately 30% of snakes had stomach contents (Table 2). In contrast, only 4.3% and 11.1% of females and males, respectively, had stomach contents in the period from April to November. In December nearly half of males had stomach contents, whereas no more than 14.4% of females had prey in stomachs. Both males and females predominantly depended on frogs in January-March and December (Fig. 2). Between April and November, the snakes more frequently depended on other vertebrate taxa (reptiles, birds, and mammals) than in the

TABLE 1. Stomach contents of *Ovophis okinavensis*. Numerals in table indicate the individual numbers of prey items followed by ratios (%) in parentheses.

Taxon			Male	Female	Total
Amphibia	Anura	*Rana narina*	59 (18.6)	93 (64.6)	152 (33.0)
		Rana sp. A*	220 (69.4)	24 (16.7)	244 (52.9)
		Rana ishikawae	1 (0.3)	2** (1.4)	3 (0.7)
		Rana holsti	1 (0.3)	0	1 (0.2)
		Rhacophorus viridis	5 (1.6)	1 (0.7)	6 (1.3)
		Buergeria japonica	1 (0.3)	0	1 (0.2)
		Unidentified frog	11 (3.5)	10 (7.0)	21 (4.6)
Reptilia	Lacertilia	*Japalura polygonata*	1 (0.3)	1 (0.7)	2 (0.4)
	Serpentes	*Achalinus werneri*	1 (0.3)	0	1 (0.2)
		Amphiesma pryeri	0	1 (0.7)	1 (0.2)
Aves	Passeriformes	*Anthus hodgsoni*	0	1 (0.7)	1 (0.2)
		Cettia diphone	2 (0.6)	0	2 (0.4)
		Erithacus cyanurus	1 (0.3)	1 (0.7)	2 (0.4)
		Luscinia calliope	1 (0.3)	0	1 (0.2)
		Turdus pallidus	1 (0.3)	0	1 (0.2)
		Unidentified bird	0	2 (1.4)	2 (0.4)
Mammal	Insectivora	*Crocidura watasei*	10 (3.2)	7 (4.9)	17 (3.7)
	Rodentia	*Rattus rattus*	0	1 (0.7)	1 (0.2)
		Rattus sp.	1 (0.3)	0	1 (0.2)
	Chiroptera	*Murina ryukyuana*	1 (0.3)	0	1 (0.2)
Total			317	144	461

* Formerly referred to as *Rana okinavana* (see Matsui, 2007).
** One of these frogs was found just grasped by a snake, but eventually the snake released the frog.

TABLE 2. Seasonal changes in the frequency (%) of snakes with stomach contents. Numerals in each set of parentheses are the number of snakes with stomach contents/the number of snakes examined.

Sex	Season		
	Jan-Mar	Apr-Nov	Dec
Female	31.3	4.3	14.4
	(90/288)	(2/46)	(15/104)
Male	26.6	11.1	48.4
	(66/248)	(6/54)	(133/275)
Total	29.1	8.0	39.1
	(156/536)	(8/100)	(148/379)

other two seasons (Fisher test, both P< 0.0001). Although males tended to have more *Rana* sp. A than females in December (male, 87.3%, female, 74.1%), this difference was not statistically significant (Fisher test, P= 0.077).

In both males and females, there were no clear alterations in diet with growth (Fig. 3). All four classes of terrestrial vertebrates (amphibians, reptiles, birds, and mammals) seemed to be fairly evenly distributed in the diet over the size ranges of snakes. Nonetheless, mean SVL of snakes that had frogs was slightly but significantly larger than that of snakes with mammals in their stomach (ANOVA, df=3, 476, F=3.918, P<0.01; Tukey-Kramer test, P<0.05; frogs, x̄±SE=474.8±2.4, mammals, 441.0±12.6; males and females were combined because of small sample size of reptiles and birds). In both sexes, no significant differences were recognized in SVL between
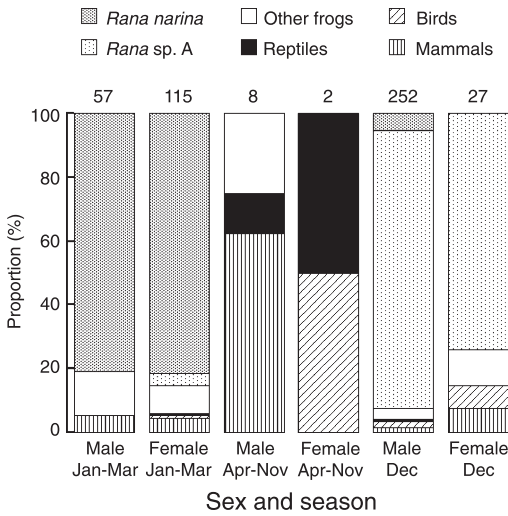
FIG. 2. Seasonal changes in the composition of prey items of male and female *Ovophis okinavensis*. Numerals above columns are sample sizes.
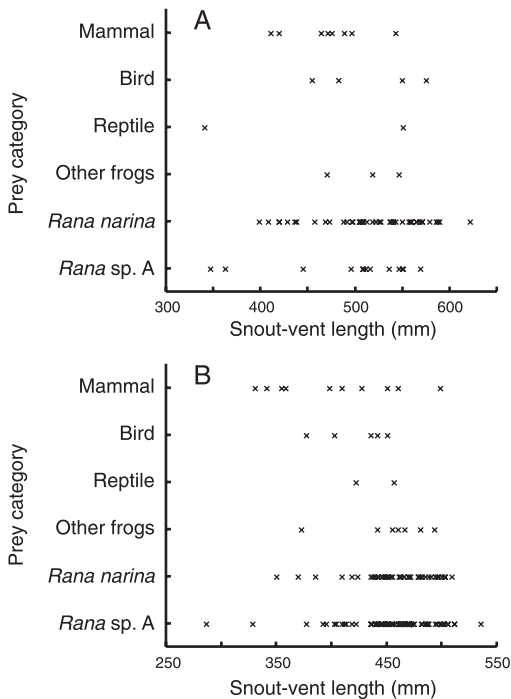

FIG. 3. Relationships between snout-vent length and prey taxa in female (A) and male *Ovophis okinavensis* (B).

snakes that had *R. narina* and *Rana* sp. A in their stomach (t-test, male, df=119, t=0.491, P=0.624; female, df=61, t=1.314, P=0.194).

There was no significant correlation between snake SVL and prey SVL (Kendall τ=0.098, P=0.077: Fig. 4A). Snakes smaller than 380 mm in SVL tended to eat only small prey (around 40 mm in SVL), but larger snakes sometimes consumed even smaller prey. The ranges of SVL of prey items consumed by snakes larger than 400 mm seemed to be nearly constant, and there were no clear sexual differences in the size range of prey items. On the other hand, there was a significant positive correlation between snake MHW and prey head width (τ=0.346, P<0.0001; Fig. 4B). Nonetheless, there were no tendencies to drop small-sized prey from the diet of large snakes. There was a significant, but weak positive correlation between snake BM and prey BM (τ=0.193, P=0.0012; Fig. 5A). Prey mass consumed by each snake ranged from 1.5 to 28.1% of the snake's body mass with mean of 5.2% (SD=4.4). There were no significant differences in relative prey width (prey head width/snake MHW) between prey swallowed head first and hind first (df=145, t=1.51, P=0.134; head first, x̄±SE=0.529±0.011, hind first, 0.555±0.012; Fig. 4B).

Multiple prey items were often found in a single snake stomach. Maximum number of prey items per stomach was nine, and approximately 44% (107/244) of snakes had more than one prey items. Body mass of partially digested frogs (*R. narina* and *Rana* sp. A) with an intact tibia bone was estimated using regression lines between tibia length and body mass obtained from undigested frogs (males and females of each species were treated separately), and total prey body mass (TPM) was calculated for each snake. TPM varied from 2.4 to 66.5 g and was significantly, but weakly correlated with snake BM (Kendall τ=0.201, P=0.0007; Fig. 5B). There were significant differences in TPM between males and females (Welch t-test, df=1, 47.65, t=2.32, P=0.0249; males, 12.8±1.0 g, female, 19.7±2.8 g). TPM consumed by each snake varied from 1.5 to
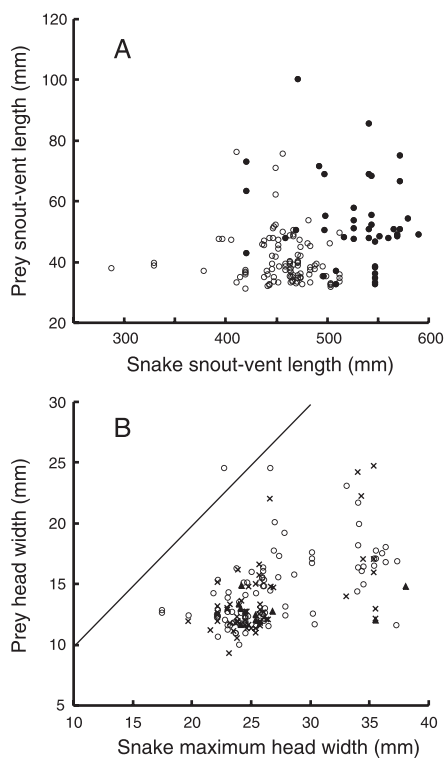
FIG. 4. Relationships between size of *Ovophis okinavensis* and that of prey items. A, snout-vent length of male (open circles) and female (closed circles) snakes vs. that of prey. B, head width of snake vs. head width of prey animals that were swallowed hind first (open circles), head first (closed triangles), and midbody first (crosses). The line shows the position where prey head width is equal to snake head width.
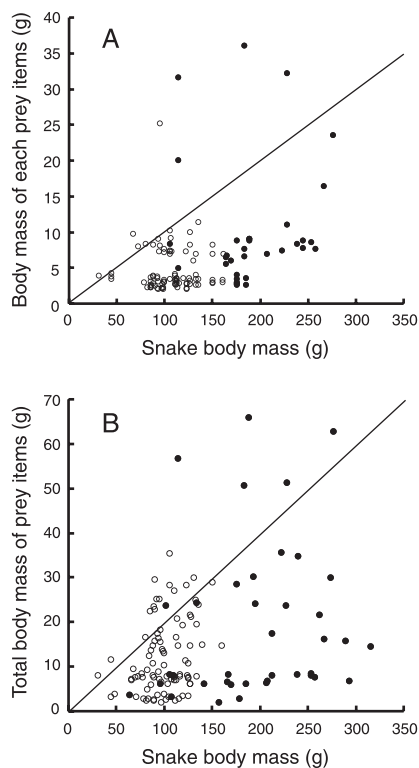

FIG. 5. Relationships of body mass of *Ovophis okinavensis* with that of each prey item (A) and total body mass of prey items from each stomach (B). Lines in A and B show positions where individual prey mass is equal to 10% of snake body mass and where the total prey body mass is equal to 20% of snake body mass, respectively. Open circles, male; closed circles, female.

50.5% of snake BM. There were no significant differences in relative TPM (TPM/snake BM) between the sexes (t-test, df=127, t= 0.947, P=0.345; male, 12.6±0.8%; female, 11.0±1.7%).

DISCUSSION

Ovophis okinavensis in the present study area exploited 17 species of animals that cover all four extant terrestrial vertebrate classes occupying diverse ecological niches, from semi-fossorial snakes, through semiaquatic frogs, terrestrial snakes and rodents, arboreal lizards,

to aerial bats and birds. This evidence shows that *O. okinavensis* is, at least qualitatively, a generalist feeder. However, vast majority of food items (86%) were comprised of only two species of frogs, *R. narina* and *R.* sp A, indicating that snakes in this population heavily depend on frogs. This high dependency on frogs, particularly between December and March, is obviously due to the exploitation of aggregated frogs that explosively breed at restricted sites along streams in winter (also see Mori et al., 2002, 2009). Possible advantages of temporarily and spatially limited, but abundant food resource, such as higher growth rate, better body condition, and longer life

span, would be worthy for pursuing in a future study.

A presumed key innovation in the evolution of viperid snakes is the improved ability of ingesting large prey, which was accomplished by structural modifications of jaws and related architectures (Pough and Groves, 1983; Greene, 1992; but see Cundall and Deufel, 2006). In this respect, *O. okinavensis* seems to provide an exceptional case. Although individual *O. okinavensis* often had multiple prey items (up to nine frogs) simultaneously, mean BM of each prey item was 5.2% of snake BM, which is much smaller than that of other vipers and even snakes of other families (Greene, 1992; Sazima, 1992; Martins et al., 2002; Rodríguez-Robles, 2002; Glaudas et al., 2008). However, this may not necessarily indicate inability of *O. okinavensis* in swallowing large prey. A recent report on predation by *O. okinavensis* observed in the field near our study site showed that a juvenile *O. okinavensis* swallowed a frog, whose BM was 49.4% of its predator's BM (Masunaga et al., 2008). Thus, the consumption of relatively small prey by *O. okinavensis* in the present study site may simply reflect limitation of the size of locally available prey animals. It is interesting to note that, although anurophagy in snakes is often associated with the evolution of enlargement of feeding apparatus to increase gape size to enable swallowing of bulky frogs (Vincent et al., 2006; Mori and Vincent, 2008), *O. okinavensis*, which predominantly exploits frogs, does not seem to face such a functional challenge (see also Vincent and Mori, 2008) and does not enjoy the advantage of the presumed viperid characteristic for swallowing large prey. High dependency on frogs has also been reported in some populations of *Viridovipera stejnegeri* in Taiwan (Creer et al., 2002) and several species of *Trimeresurus* (sensu lato) in eastern and southeastern Asia (Orlov et al., 2002), but their size relationships are yet unknown. On the other hand, species of *Causus*, a basal group of viperids, have been characterized by anurophagy and the consumption of massive prey items (Ineich et al., 2006). More quanti-

tative studies are needed to discuss possible feeding adaptation of Asian pitvipers that depend predominantly on frogs.

Another common trophic feature of vipers is the ontogenetic shift from ectothermic to endothermic prey (Mushinsky, 1987; Greene, 1997; Shine and Wall, 2007). For example, most members of *Crotalus* reportedly shift diet from lizards to mammals (Klauber, 1972; Campbell and Lamar, 1989). Some Asian pitvipers also show similar ontogenetic dietary shifts (*Protobothrops flavoviridis*, Nishimura et al., 1991; *Calloselasma rhodostoma*, Daltry et al., 1998; *Trimeresurus gracilis*, Lin and Tu, 2008). Many species of *Bothrops*, which are dietary generalists, drop ectothermic animals from their diet with growth (Martins et al., 2002). With respect to *O. okinavensis*, our result may reflect the tendency opposite to the general viperid pattern, because snakes that had frogs in the stomach were slightly larger in SVL (ca. 34 mm) than those that had mammals. Even so, however, body size of the snakes largely overlapped among prey categories, leaving the tendency of ontogenetic dietary shift rather obscure. In the analysis of generalist species of the Latin American genus *Bothrops*, Martins et al. (2002) indicated that the species that do not show ontogenetic dietary shifts are small-sized (mean adult total length=593–742 mm). The absolute small body size of *O. okinavensis* that would decrease the possible size range of prey may be partially responsible for the lack of clear ontogenetic dietary shift (Shine and Wall, 2007). In addition, the high dependency on locally abundant frogs throughout almost whole life history may contribute to obscure the possible dietary shifts, that is, specialization on relatively small prey may prevent an ontogenetic shift of feeding (see Shine and Wall, 2007). Studies on *O. okinavensis* from other localities with different prey availability are desired to examine whether the lack of clear ontogenetic dietary shift mentioned above is a specific characteristic of *O. okinavensis* or it reflects a more limited local phenomenon.

Although weak positive correlations were

found, as in some comparable studies on other snakes (Shine, 1991a; Arnold, 1993), between the snake and prey sizes (represented by the maximum width or mass), there were no clear tendencies to increase the lower prey-size limit as snake size becomes larger. This results in an ontogenetic telescope pattern (after Arnold, 1993) in a relationship between snake size and prey size. Although this pattern has been considered less common in snakes in general (Arnold, 1993; Glaudas et al., 2008), it has been known in several vipers including four generalist species of *Bothrops* (Martins et al., 2002). Continuous exploitation of small prey by larger *O. okinavensis* may be due to the high dependency on the abundant frog (*Rana* sp. A). Arnold (1993) indicated that, from the viewpoint of optimal foraging theory, prey selection is determined by the probabilities of encounter, capture, and ingest a prey animal and costs of these phases. In the case of *O. okinavensis* in the present study area, the high availability of the small-sized prey (i.e., *Rana* sp. A) and relative easiness of capturing and handling the frog, as well as the ability to efficiently swallow small animals in vipers (Pough and Groves, 1983) and the low energy costs of striking, handling, and ingesting prey in snakes in general (Feder and Arnold, 1982; Cruz-Neto et al., 1999, 2001), may be reasons why the snake retains small animals as valuable prey even after growing large.

Sexual dimorphism in head size has been demonstrated in many groups of snakes including vipers (Shine, 1991b; Vincent and Herrel, 2007) and is usually considered to be a result of natural selection that leads to intersexual dietary divergence (Shine, 1991b). The male biased feeding on *Rana* sp. A and the female biased feeding on *R. narina* may seemingly coincide with this general explanation because female *O. okinavensis*, which has larger SVL and larger MHW relative to SVL than males, more frequently exploits the larger species of frog (*R. narina*). However, the other head size measurements, JL and IOD, did not differ between the sexes. Actually, both males and females did eat both species of frogs (Table 1), and there seems to be no relationship between the size of the snake and the tendency of eating these frogs (Fig. 3). Thus, it is unlikely that this sexual dietary divergence is caused by natural selection acting to reduce intersexual competition for food resources. In fact, a proximate factor that caused this intersexual difference is obviously a highly biased appearance of males in one specifically restricted breeding site of *Rana* sp. A, where few females were observed during the short breeding period of this frog (Mori and Toda, unpublished data). Detailed investigation of intersexual differences of foraging behavior and other possibly relevant ecological factors are needed to elucidate why females of *O okinavensis* neglect such a highly rich food resource.

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