WINTER ACTIVITY OF THE HIME-HABU (*OVOPHIS OKINAVENSIS*) IN THE HUMID SUBTROPICS: FORAGING ON BREEDING ANURANS AT LOW TEMPERATURES

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ABSTRACT: Snakes are ectothermic and rely on external heat sources to elevate their body temperature to levels required for various activities. Because of this constraint, snakes living at high latitudes and/or elevations cease their activity during cold weather, and in some cases exhibit physiological adaptations to the cold climate. *Ovophis okinavensis* is a small, nocturnal pitviper found in the subtropical region of the Ryukyu Archipelago, Japan, where the ambient temperature has a distinct seasonal fluctuation. We studied seasonal activity patterns, body temperatures, and food habits of *O. okinavensis* along a mountain stream from December 1996 to March 2000. Preliminary observations were also made with captive snakes to test the hypothesis that *O. okinavensis* has a physiological adaptation to efficiently digest prey at low temperatures. We found that *O. okinavensis* is most active at night during the cool season (from December to February), when two species of ranid frogs (*Rana narina* and *R. okinavana*) aggregate at a stream for reproduction. The body temperature of *O. okinavensis* ranged from 11.2 to 23.8°C ($\bar{x}$ = 16.1°C). Ninety-eight percent of the stomach contents consisted of frogs, and 37.0 % and 54.7 % were identified as *R. narina* and *R. okinavana*, respectively. The appearance of *O. okinavensis* coincided with breeding aggregations of these frogs, and extensive predation on the frogs by the snakes strongly suggests that winter activity in *O. okinavensis* at low body temperatures is associated with foraging. A comparison of digestion rates of *O. okinavensis* with those reported for other snakes failed to support our hypothesis that at low temperatures *O. okinavensis* digests prey faster than other snakes. An extensive literature survey showed, however, that the active body temperature of *O. okinavensis* in winter is lower than values reported for other viperids. We assume that high activity in *O. okinavensis* at low body temperatures evolved to exploit anuran breeding aggregations in winter. This study illustrates the adaptation of a viperid to cool temperatures in a humid, subtropical zone.

INTRODUCTION

Snakes are ectotherms and thus rely on ambient heat sources to attain body temperatures to regulate their physiological and behavioral activities (Huey, 1982; Lillywhite, 1987). Despite the constraints of ectothermy, snakes have successfully radiated habitats worldwide except for extreme latitudes, high elevations, and some oceanic islands. In lowlands of the humid tropics, constantly high ambient temperatures enable snakes to be active throughout the year (Shine and Madsen, 1996; Daltry et al., 1998). At higher latitudes and/or elevations, snakes show a variety of adaptations to low temperatures; the most prominent is hibernation, a winter dormancy associated with metabolic depression (Spellerberg, 1976; Gregory, 1982). In areas with moderate winters, such as the subtropics, some species may hibernate while others are inactive only during the coldest periods (Ashton and Ashton, 1981; Gregory, 1982). As a consequence, snakes living in areas where the ambient temperature fluctuates show seasonal changes in activities and usually become less active in cooler seasons (Gibbons and Semlitsch, 1987).

The body temperature that snakes exhibit during activity can range from 10 to 40°C, but the preferred body temperature is relatively uniform, and is usually between 25 and 35°C (Avery, 1982; Lillywhite, 1987). Although some snakes at high latitudes and/or elevations may show lower body temperatures compared to conspecifics at lower latitudes and/or elevations (Vitt, 1974; Henderson and Henderson, 1995), both northern and montane species regulate their body temperature to ca. 30°C when heat sources are accessible (Gibson and Falls, 1979; Scott and Pettus, 1979; Peterson, 1987; Tuniyev and Volcik, 1995). Most of these data are derived from studies on diurnal species, however, and only a few studies focus on the thermal biology of snakes that are commonly nocturnal (e.g., Henderson and Henderson, 1995; Secor, 1995; Daltry et al., 1998; Dorcas and Peterson, 1998; Webb and Shine, 1998).

The Hime-Habu (*Ovophis okinavensis*) is a short, stout-bodied crotaline snake found on the subtropical islands of the Okinawa and Amami groups, Ryukyu Archipelago, Japan (Fig. 1; Plate 4b). Although in this paper we treat the Hime-Habu as a member of the genus *Ovophis* (as per McDiarmid et al., 1999), recent phylogenetic analyses indicate that inclusion of the Hime-Habu into *Ovophis* renders the genus paraphyletic (see Tu et al., 2000; Parkinson et al., this volume). Until further research is accomplished, the former combination, *Trimeresurus okinavensis*, may be more appropriate.

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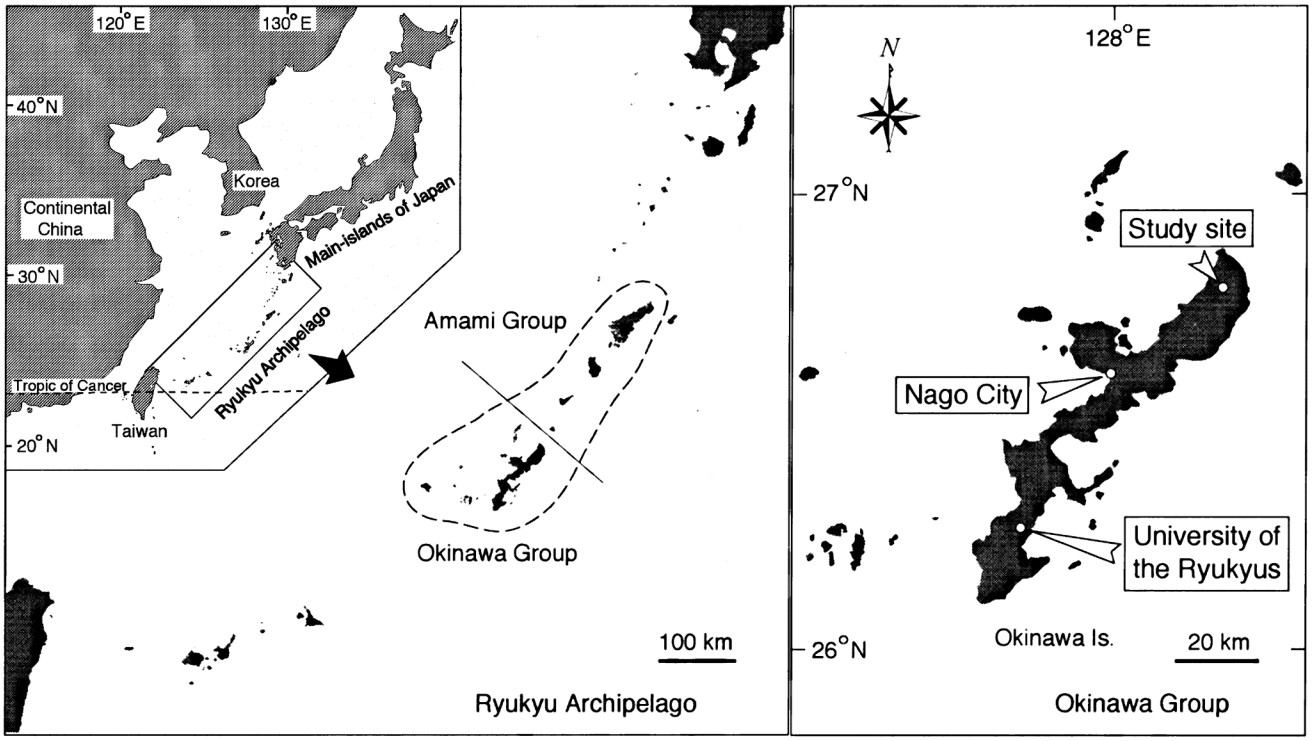

Fig. 1. Map showing the location of the study site. The Ryukyu Archipelago is located in the subtropical zone. *Ovophis okinavensis* is distributed in the Okinawa and Amami island groups.

Ovophis okinavensis is considered to be essentially terrestrial and nocturnal (Koba, 1962; Takara, 1962; Moriguchi, 1989), and its diet consists of frogs, lizards, snakes, birds, and small mammals (Mori and Moriguchi, 1988). Preliminary ecological studies by Ikehara and Akamine (1976) and Moriguchi (1989) showed that in the northern mountains of Okinawa Island, *O. okinavensis* is active throughout the year and is observed most frequently from winter to early spring when the air temperature is below 20°C. Moriguchi (1989) surmised that the high activity of *O. okinavensis* during the cool season is associated with foraging activity and the intensive breeding aggregations of syntopic frogs.

We studied the seasonal appearance and food habits of *O. okinavensis* in the northern mountains of Okinawa Island where two species of frogs, *Rana narina* and *R. okinavana*, breed in winter. Field surveys were conducted primarily in winter to investigate the activity of *O. okinavensis* in a cool environment and its relation to anuran breeding activities. We also examined the body temperature of *O. okinavensis* to characterize its thermal propensity.

In addition to field surveys, laboratory experiments were conducted to examine the possible physiological adaptation of *O. okinavensis* to low temperatures. Considering that various adaptations to cold temperatures have been reported for other species of snakes (Spellerberg, 1976), we questioned whether winter foraging activity in *O. okinavensis* represents a physiological adaptation to low temperatures. Duration of digestion is known to be temperature dependent (i.e., the lower the temperature, the longer the period of digestion; see Skoczylas, 1970; Naulleau, 1983a, b). Thus, we hypothesized that digestion at low temperatures is more rapid in *O. okinavensis* than in snakes that are active at higher body temperatures. To test this hypothesis we measured, under relatively low ambient temperatures, digestion rates in *O. okinavensis* feeding on frogs by using X-ray photography.

MATERIALS AND METHODS

Field Studies

Field surveys were carried out along the upper stream of the Zatsun River (26°48' N, 128°16' E, ca. 350 m above sea-level) near the peak of Mt. Nishimedake, Kunigami Village, on the northern part of Okinawa Island (Fig. 1). Vegetation covering the riverbanks was primarily humid-subtropical broadleaf evergreen forest. The mean monthly relative humidity and precipitation, recorded by the Japan Weather Association, Okinawa Branch at Nago City (ca. 40 km southwest of the study site; Fig. 1), exceed 70% and 100 mm, respectively, throughout the year, and the air

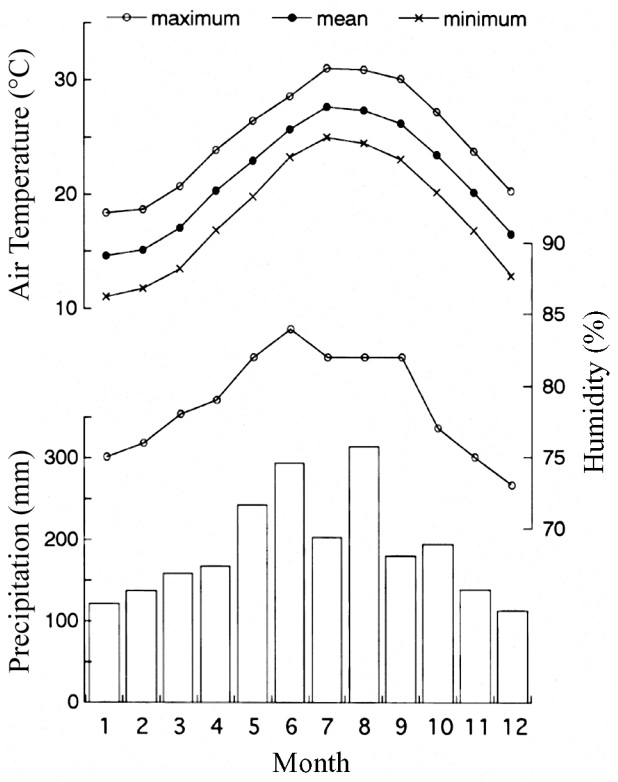

Fig. 2. Seasonal changes of meteorological features in Nago City, 40 km southwest of the study site (Fig. 2). Monthly maximum, mean, and minimum values are shown for air temperature. Monthly averages are shown for relative humidity and precipitation. Data originated from the Weather Calendar of Okinawa, 1995, published by the Japan Weather Association, Okinawa Branch.

temperature fluctuates seasonally but rarely falls below 10°C (Fig. 2).

The study area was a 350 m strip along a stream close to its headwaters (hereafter referred to as the main stream), and a 150 m strip along a small tributary that flows into the main stream 200 m from its upper end, which made the study route roughly "T-shaped." The main stream was about 3–30 cm deep and 1–4 m wide, and its current was relatively slow. The streambed consisted of pebbles, boulders, and bedrock, and was shaded by broadleaf evergreens. The banks of the stream were steep, and approximately 100 m from the upper end of the main stream was a waterfall ca. 3 m in height. Most of the tributary was less than 3 cm deep, and thus water flow was slower than in the main stream; the bottom of the tributary was covered with small pebbles and sand. Water along the entire stream was clear except after heavy rains.

Five species of stream-dwelling frogs were present in the study area (Maeda and Matsui, 1999). Three of them (*Rana ishikawae*, *R. narina*, and *R okinavana*), breed in winter (December to March), and the other two (*R. holsti* and *R. namiyei*), breed in spring and summer (May to September) (Utsunomiya et al, 1983; Maeda and Matsui, 1999). *Rana narina* and *R. okinavana* are occasionally referred to as "explosive breeders" because they show concentrated spatial and temporal reproductive activities (Sengoku, 1983; Sengoku et al., 1996).

Our studies were conducted from December 1996 to March 2000. We visited the study site primarily from December to March when breeding activities for *R. narina* and *R. okinavana* were anticipated. We made a total of 120 night surveys as follows: January (26), February (20), March (15), April (1), May (3), June (2), July (3), August (3), September (4), October (3), November (3), and December (37).

When anuran breeding activity was anticipated, we made surveys on more than five consecutive nights, but at other times surveys were conducted for three consecutive nights. Three or four people usually conducted each survey by walking slowly (< 500 m/h) along the stream between 1900 and 0600 h. The main stream and tributary were surveyed twice per night except for the following three periods: (1) December 1996, when the surveys were conducted from two to four times per night and the route of the tributary was restricted to 100 m, (2) September 1997, when only the main stream was surveyed, and (3) a night in March 2000, when we only conducted a single survey. We used flashlights to search for *O. okinavensis* along the streambed and its environs, as well as the banks of the stream to approximately eye-level. We searched fissures in rocks, crevices on ledges, and burrows on the banks, but never turned over rocks or other objects.

When a snake was located, we recorded several aspects of its behavior, and when captured with a snake hook it was gently coaxed into a 50 or 60 cm long acryl tube for safe handling and processing. Cloacal body temperature (BT) was measured with a thermistor (Takara, Digimulti D611). After processing, the snake was allowed to crawl out of the tube into a carrying box. The ambient air temperature 1 m above the ground (AT) and substrate temperature (ST) where the snake was first sighted were also recorded. When a snake was found immersed in water, the water temperature was treated as the ST.

Snakes were brought to the Yona Experimental Forest Station, University of the Ryukyus, approximately 12 km from the study site, where they were measured for snout-vent length (SVL) and body mass (BM), sexed, checked for stomach contents, and indi-

vidually marked for future identification (e.g., ventral scale clipping and painting numbers on the dorsal surface of head and posterior body). In addition, after August 1998, small (11.5 x 2.2 mm) passive integrated transponder (PIT) tags were injected under the skin for identification. Sex was determined by using a sexing probe, by everting hemipenes, or by examining the external shape of the tail base. Stomach contents were examined by palpation and forced-regurgitation. Frogs recovered by forced-regurgitation were identified and force-fed back to the snakes. Unidentified food items and animals other than frogs were preserved in formalin for later examination. Finally, each snake was released at the site of capture within 24 h after collection. The data are presented as means ± one standard deviation.

When we found that a snake had been collected within two weeks (determined visually by the painted numbers; see Plate 4c), to minimize disturbance we usually recorded only its identification number, time, location, and behavioral data. On the last night when consecutive surveys were carried out, however, we captured snakes irrespective of the intervals from previous captures, to examine their stomach contents if frog breeding aggregations were suspected during that period. Prey animals, confirmed by direct observations of feeding behavior of *O. okinavensis*, were recorded as food items.

In the following analyses, we did not consider the potential differences between the sexes or among age classes of *O. okinavensis*. Sexual differences in appearance, body temperature, and food habits will be presented in another paper.

Examination of Digestion Rates

Digestion rates were measured experimentally to examine the possible physiological adaptation of *O. okinavensis* to low temperatures. Three female (BM = 82, 140, and 168 g) and three male (BM = 75, 79, and 106 g) *O. okinavensis* were collected from northern Okinawa Island, 5–15 km from the study site. They were individually maintained in plastic enclosures [L28 x W17 x H17 cm (for males) and L35 x W20 x H21 cm (for females)] with paper as a substrate, and each with a water container. The enclosures were placed outdoors in shade on the side of the building of the College of Science, University of the Ryukyus, in southern Okinawa Island (ca. 80 km southwest of the study site; Fig. 1). The snakes were fasted for at least 10 days, and palpation confirmed that no stomach contents were present prior to the experiment.

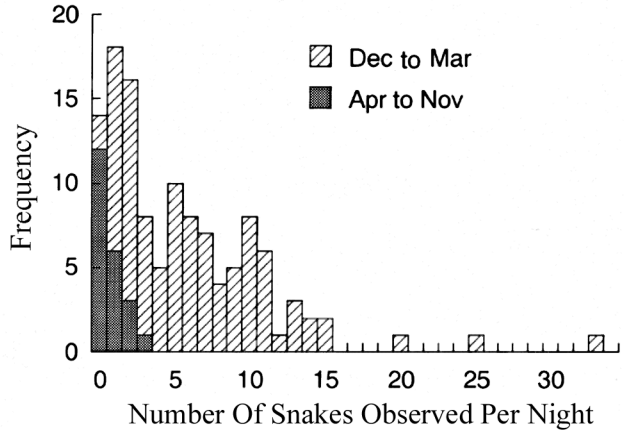

Fig. 3. Frequency distribution of the number of *Ovophis okinavensis* observed per night.

Three *R. narina* (mean BM = 7.6 g ± 0.8) were introduced into each enclosure at 1950 h on 16 February 1997. By 1000 h on 17 February, each of the females had consumed all three frogs, whereas males consumed 1–3 frogs. At 1200 h the remaining frogs were force-fed to the corresponding males. Mass ratios of the total frogs consumed were 0.23, 0.30, and 0.31 for males, and 0.13, 0.16, and 0.28 for females. The enclosures were maintained outdoors in shade for 17 days. The ambient air temperature during the first week fluctuated from 10.0 to 20.0°C, and for the following 10 days from 12.0 to 24.0°C.

X-ray photography was used to assess digestion rates from 2300 h on 18 February until bony elements of frogs were not detectable, or 5 March, whichever came first. We took X-rays of the snakes at ca. 24 h intervals. In this procedure the snakes were gently removed from their enclosures with a snake hook and transferred into shallow, transparent, plastic containers that were placed on the X-ray photographic apparatus (SOFRON SRO-405A). Photographs were taken using soft radiation, with 40 kV tension, intensity of 5 mA, 35 cm distance, and exposure of 110–150 sec. *Ovophis okinavensis* is a docile species, and the snakes remained motionless without any restraint or anesthetization during the procedure.

Because the exact time of feeding was unknown, we assumed 1200 h on 17 February as the feeding time. We defined completion of digestion as the halfway point between the time when no frog bones were visible on the X-ray and the time of the previous X-ray.

RESULTS

Field Observations

We marked 174 (94 males, 80 females) *O. okinavensis*. Mean SVL and BM were 445 ± 44.3 mm

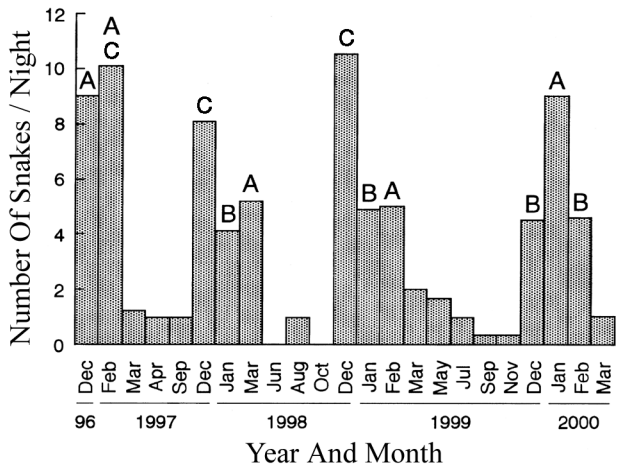

Fig. 4. Seasonal fluctuation of the number of *Ovophis okinavensis* observed at the study site. Mean number of snakes per night is shown for each month. (A) The survey was conducted within two weeks after frog breeding aggregations (*Rana narina* for January to March and *R. okinavana* for December). (B) The survey was conducted more than a week before a breeding aggregation of the frogs. (C) The breeding aggregation of the frogs occurred during the survey period.

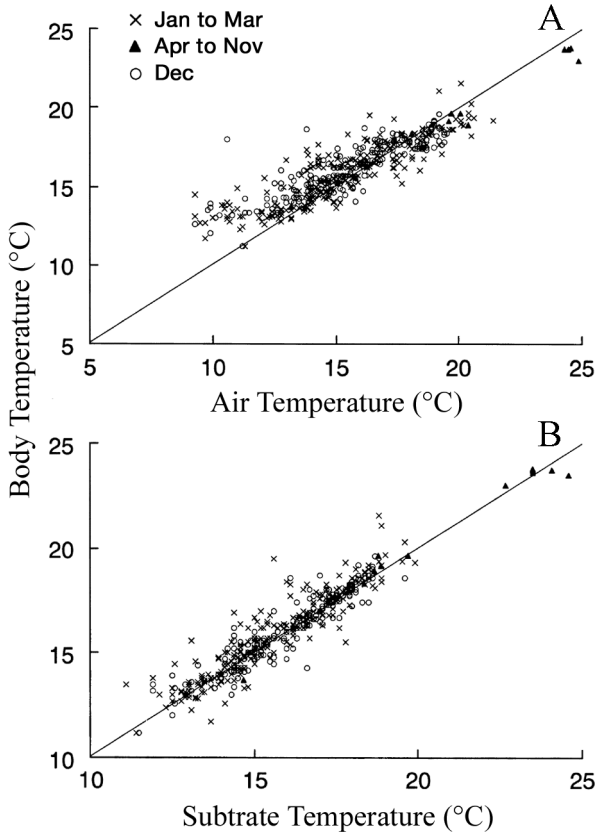

Fig. 5. Thermal relations of *Ovophis okinavensis* observed at night. (A) Relation between air temperature and body temperature. (B) Relation between substrate temperature and body temperature.

(range 277–511 mm) and 97 ± 29.4 g (range 21.5–202 g) for males, and 506 ± 71.5 mm (range 247–646 mm) and 185 ± 72.1 g (range 16.8–391 g) for females, respectively. Approximately 60% of the snakes were sighted more than once during the study period, and a total of 651 sightings (356 males, 254 females, and 41 unsexed snakes) were recorded.

The number of snakes observed per night varied from 0–33 (each individual sighted more than once per night was counted as one) (Fig. 3). The mean number from December to March (the potential breeding season of *R. narina* and *R. okinavana*, hereafter referred to as the winter period) was 6.5, whereas from April to November (hereafter referred to as the non-winter period) the mean number was 0.7. During the latter period, no snakes were found in 12 of 22 survey nights. On the other hand, at least one snake was sighted in 96 of 98 nights during the winter period. The difference in the number of snakes per night between the two periods was highly significant (*U*-test, $Z = 6.31$, $P < 0.0001$).

The monthly average number of snakes encountered per night fluctuated seasonally (Fig. 4). During the winter period, *O. okinavensis* was observed more frequently, and in non-winter an average of less than two snakes were observed per night.

In winter, the number of snakes observed seemed to be affected by the temporal relationship between the breeding aggregations of frogs and the survey dates. Every year, breeding aggregations of *R. okinavana* occurred in December, but the date varied from 1 to 25 December. Extensive breeding activity (calling by males, amplexus, and oviposition), however, was confined to one or two nights. Three predominant breeding sites in the study area were confirmed for *R. narina*. Breeding aggregations of *R. narina* fluctuated from year to year, and also varied among the three sites within a given year (from 31 December to 20 February). At a particular site, extensive breeding activities of *R. narina* also seemed to be confined to one or two nights. When surveys were conducted within two weeks after or one week prior to a breeding aggregation of the frogs, we observed five to ten snakes per night (Fig. 4). On the other hand, when surveys were made more than two weeks after the latest aggregation and more than a week prior to the next one, only four or five snakes were observed per night.

Body Temperature

The BT of *O. okinavensis* ranged from 11.2 to 23.8°C ($\bar{x}$ = 16.1°C, N = 446), with most values

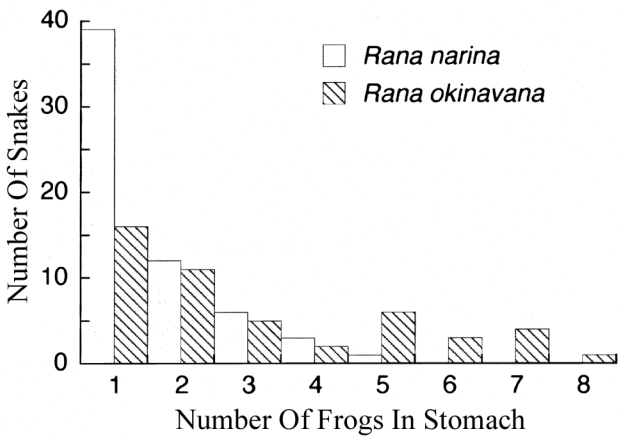

Fig. 6. Frequency distributions of number of frogs contained in stomachs of *Ovophis okinavensis*. Snakes with unidentified prey or frogs other than *Rana narina* and *R. okinavana* were excluded. No snake contained *R. narina* and *R. okinavana* in its stomach simultaneously.

ranging between 12 and 20°C (Fig. 5). Minimum AT was 9.3°C. For the following statistical analyses of temperature relationships, only one data set (initial capture) was used for each snake to ensure statistical independence when multiple data were obtained from a single individual, except for the non-winter period for which data of recaptured snakes were also used because of the small sample size (but no identical individuals were observed more than once in this period). Relationships between AT and BT, and between ST and BT were compared among snakes collected in December, from January to March, and in the non-winter period.

Body temperature was highly correlated with AT in all periods (December, $r = 0.88$, $df = 67$, $t = 14.9$, $P < 0.001$; January to March, $r = 0.88$, $df = 100$, $t = 18.5$, $P < 0.001$; non-winter, $r = 0.99$, $df = 10$, $t = 19.3$, $P < 0.001$; Fig. 5). The slopes significantly differed among the periods (ANCOVA, $F_{2, 177} = 4.42$, $P = 0.013$). Multiple comparisons revealed that the slope was largest in non-winter and smallest in December (all, $P < 0.05$). In any period, the slope was significantly different from both 0 and 1 (all $P < 0.001$). The snakes tended to keep higher BT than AT when AT was relatively low, and lower BT than AT when AT was relatively high.

Body temperature was significantly correlated with ST in all periods (December, $r = 0.90$, $df = 67$, $t = 16.8$, $P < 0.001$; January to March, $r = 0.66$, $df = 100$, $t = 8.8$, $P < 0.001$; non-winter, $r = 0.99$, $df = 10$, $t = 18.1$, $P < 0.001$; Fig. 5). There were no significant differences in the relationship of BT to ST among the three periods (ANCOVA, slope: $F_{2, 177} = 0.12$, $P > 0.05$; elevation: $F_{2, 179} = 0.22$, $P > 0.05$). Thus, analyses were also conducted by pooling all data, in which BT was significantly correlated with ST ($r = 0.83$, $df = 181$, $t = 20.3$, $P < 0.001$). Slope significantly differed from 0 ($F_{1, 181} = 413.3$, $P < 0.001$), but not from 1 ($F_{1, 181} = 1.25$, $P > 0.05$). Body temperature was significantly higher than corresponding ST (paired *t*-test, $df = 181$, $t = 5.5$, $P < 0.001$), although mean BT (15.8°C) was only slightly higher than mean ST (15.5°C).

Stomach Contents

A total of 265 prey items were confirmed from 118 snakes (Table 1). All but six prey items were frogs, of which *R. narina*, *R. okinavana*, *R. ishikawae*, and unidentified frogs composed 37.0 %, 54.7 %, 0.8 %, and 5.3 % of the prey items, respectively. The remaining six food items consisted of two partially digested shrews (*Crocidura watasei*) and four mostly digested passeriform birds (one *Turdus pallidus*, two *Cettia diphone*, and one unidentified small bird; identifications based on tarsus length and distributional range).

From January to March 27.6 % (63/228) of the snakes had at least one prey item in their stomachs, and 89.1 % (90/101) of the prey items were *R. narina* (Table 1). On the other hand, 30.1 % (55/179) of the snakes had at least one stomach content in December, and 87.8 % (144/164) of the prey items were *R. okinavana* (Plate 4c). From April to November, none of the snakes examined had stomach contents (N = 13).

The frequency of snakes having prey in their stomachs varied considerably, even within the winter period (Table 1). When surveys were conducted more than a week before the next breeding aggregation of the frogs and more than two weeks after the previous one, less than 10 % of the snakes had stomach contents (8.4% for January to March, and 8.7% for December). In contrast, ca. 35 % of the snakes contained food in their stomachs when survey periods included the days of breeding aggregations or were conducted within two weeks after or one week before them.

Up to five *R. narina* were found in a single stomach (Fig. 6). Thirty-six percent of the snakes with *R. narina* as stomach contents contained more than one frog. Similarly, up to eight *R. okinavana* were found in a single stomach, and 66.7 % of the snakes with *R. okinavana* contained more than one frog (Fig. 6).

Digestion Rate

Two male snakes that refused to eat or ate only one frog and were force-fed, regurgitated all the frogs within 24 h. Thus, the remaining four snakes were

Table 1. Numbers of *Ovophis okinavensis* with prey in their stomachs, and prey recovered from the stomachs during each survey period. N = number of snakes. Rn = *Rana narina*; Ro = *Rana okinavana*.

Period (year/month)	N		Stomach contents				
	With prey	Total	*Rana narina*	*Rana okinavana*	Frogs[1]	Other	Total
1996. 12	16	40	0	51	2	0	53
1997. 1	8	17	11	0	0	0	11
1997. 2	23	56	31	0	5	0	36
1997. 3	0	5	0	0	0	0	0
1997. 4, 9	0	2	0	0	0	0	0
1997. 12	20	58	2	58	5	3	68
1998. 1[2]	2	34	2	0	0	0	2
1998. 3	7	22	12	0	1	0	13
1998. 6, 8, 10	0	3	0	0	0	0	0
1998. 12	17	58	5	34	0	2	41
1999. 1[2]	3	35	2	0	1	0	3
1999. 2	5	19	11	0	0	0	11
1999. 3	0	5	0	0	0	0	0
1999. 5, 7, 9, 11	0	8	0	0	0	0	0
1999. 12[3]	2	23	1	1	0	0	2
2000. 1	12	35	17	1	2	1	21
2000. 2	3	20	4	0	0	0	4
2000. 3	0	3	0	0	0	0	0
January to March							
Before breeding of Rn[2]	8	95	8	0	1	0	9
	(8.4%)		(88.9%)	(0%)	(11.1%)	(0%)	
During/after breeding of Rn	55	156	82	1	8	1	92
	(35.2%)		(89.1%)	(1.1%)	(8.7%)	(1.1%)	
Subtotal	63	228	90	1	9	1	101
	(27.6%)		(89.1%)	(1.0%)	(8.9%)	(1.0%)	
April to November	0	13	0	0	0	0	0
	(0%)						
December							
Before breeding of Ro[3]	2	23	1	1	0	0	2
	(8.7%)		(50.0%)	(50.0%)	(0%)	(0%)	
During/after breeding of Ro	53	156	7	143	7	5	162
	(34.0%)		(4.3%)	(88.3%)	(4.3%)	(3.1%)	
Subtotal	55	179	8	144	7	5	164
	(30.1%)		(4.9%)	(87.8%)	(4.3%)	(3.0%)	
Total	118	443	98	145	16	6	265
	(26.6%)		(37.0%)	(54.7%)	(6.0%)	(2.3%)	

[1]Includes 14 unidentified frogs and two *Rana ishikawae*. [2]Surveys made more than a week before or more than two weeks after breeding aggregations of *R. narina*. [3]Surveys made more than a week before the breeding aggregation of *R. okinavana*.

used for examining the digestion rate (passage time; see Lillywhite et al., this volume). The visibility of bony elements of the swallowed frogs in the X-ray photographs gradually but steadily decreased (Fig. 7). The duration of digestion seemed to be positively correlated to the total mass of the frogs relative to the mass of the snake (relative frog mass), although no statistical tests were performed due to the small sample size. Complete digestion in females that ate relative frog masses of 13%, 16%, and 28 % took 214 h, 237 h, and 364 h, respectively. With respect to a male that ate frogs with a relative mass of 31 %,

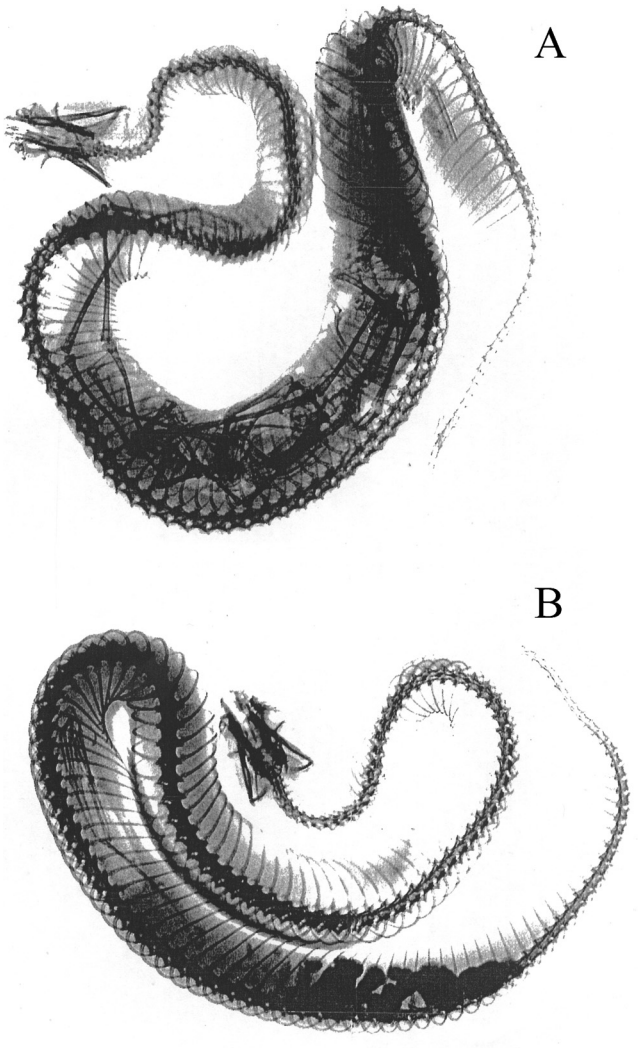

Fig. 7. X-ray photographs of a male *Ovophis okinavensis* with frogs in its stomach. (A) 59 h after feeding the bones of three frogs are clearly visible. (B) 376 h after feeding several bony elements of the hindlegs of the third frog remain visible.

small parts of bony elements were still visible 376 h after feeding (Fig. 7).

DISCUSSION

This study demonstrates that *O. okinavensis* is active in winter at temperatures mostly below 20°C. Synchrony of the snake's activity with the breeding activities of two species of frogs (*R. narina* and *R. okinavana*) and the high occurrence of these frogs in their stomachs strongly suggests that the winter activity of *O. okinavensis* is associated with foraging. Indeed, most of the snakes in the vicinity of anuran breeding sites were observed in ambush posture similar to that observed in other pitvipers (Reinert et al., 1984; Beaupre, 1995; Orlov et al., this volume; Plate 4b). Exploitation of spatially and temporally concentrated prey animals, often associated with a high frequency of capture, has been reported for several snakes (e.g., Wharton, 1969; Arnold and Wassersug, 1978; Mori et al., 1992, 1999). The rate of food intake of *O. okinavensis* in winter is also relatively high considering that ambush predation is usually associated with low rates of food intake (Greene, 1986; Shine, 1980; Secor and Nagy, 1994).

Because our data were obtained largely in the cool season, the mean BT value of active *O. okinavensis* (16.1°C) is likely underestimated. Nevertheless, we can conclude that *O. okinavensis* has a propensity to forage at relatively low temperatures. An extensive literature survey on the body temperature of vipers is presented in Table 2. Although vipers are distributed from the equator to high latitudes, their preferred BT and/or mean field BT is mostly > 25°C, and no species show a mean BT < 20°C. Interestingly, the Adder (*Vipera berus*), the northernmost ranging ophidian species, shows a high mean BT (Table 2). At least three factors may allow *O. okinavensis* to forage at a low BT. First, compared to active foraging, which requires a high BT to rapidly pursue and lunge at prey (Greenwald, 1974; Stevenson et al., 1985; Fukada, 1992), ambush foraging may not rely largely on body temperature to successfully capture prey (Secor, 1995; but see Ayers and Shine, 1997; Webb and Shine, 1998). Second, maintaining a high BT is important for active foragers that rely on rapid locomotion to escape predation, whereas ambush foragers mainly depend on crypsis (Greene, 1997), in which efficiency in predator avoidance is expected to be temperature-independent. Last, the ambient temperature in the humid subtropics seldom drops to a lethal point for snakes, so activity during the coldest season may not be as critical as it would be for snakes in temperate climates.

It would appear that the low BT of *O. okinavensis* is partially attributed to its nocturnal activity. Although many of the vipers listed in Table 2 are active in the day and at night (often seasonally dependent), except for a few species, their thermal performance during nocturnal activities has been rarely documented in detail (e.g., Daltry et al., 1998; Secor, 1995). Extensive studies on nocturnal thermoregulation are extremely limited even in other groups of snakes (*Morelia spilota*, Slip and Shine, 1988; *Corallus enydris*, Henderson and Henderson, 1995; *Charina bottae*, Dorcas and Peterson, 1998; *Hoplocephalus bungaroides*, Webb and Shine, 1998). The thermal performance of nocturnal snakes when they are active (night), and inactive (day), should be

interpreted separately. In nocturnally active snakes of the above studies, BT at night is almost as high as in diurnal species (Secor, 1995; Daltry et al., 1998) or relatively low with considerable seasonal and regional variations (Slip and Shine, 1988; Henderson and Henderson, 1995; Dorcas and Peterson, 1998; Webb and Shine, 1998). The most extreme example is in a small temperate zone erycine (Rubber Boa, *Charina bottae*) in which BT during nocturnal foraging activity is as low as 10°C (Dorcas and Peterson, 1998). Thermoregulation during nocturnal activity may be attained by specific heat-conserving behaviors such as postural adjustments and retreat site selection (Slip and Shine, 1988; Ayers and Shine, 1997; Webb and Shine, 1998), or otherwise, the snakes may not regulate their BT at all during nocturnal activity (Henderson and Henderson, 1995; Secor, 1995; Daltry et al., 1998; Dorcas and Peterson, 1998; Webb and Shine, 1998).

The relationship between BT and AT in *O. okinavensis* (i.e., higher BT than AT at low AT, and lower BT than AT at high AT), suggests that it actively thermoregulates at night. On the other hand, the high correlation between BT and ST suggests two possibilities: (1) this species is thigmothermic and thermoregulates by absorbing heat through contact with warm surfaces, and (2) this species is thermoconformic, in which variation in BT simply parallels that in ambient temperature (Pough and Gans, 1982). In the former case, *O. okinavensis* actively thermoregulates by selecting warm substrates to increase its BT when AT is low and cool substrates to decrease its BT when AT is high. In the latter case, the snake does not thermoregulate and the difference between the BT-AT relation and the BT-ST relation simply reflects the differences of cooling and heating rates between the air and substrate: at night on cool days the substrate remains hotter than air, and at night on hot days the substrate remains cooler than air. The correct interpretation for *O. okinavensis* in the study site remains unclear.

Recent studies have revealed that nocturnal snakes increase their BT while hiding in retreat sites in the daytime (Daltry et al., 1998; Dorcas and Peterson, 1998; Webb and Shine, 1998), and that nocturnally active snakes may exhibit basking behavior under direct sunlight (Slip and Shine, 1988; Dorcas and Peterson, 1998; Webb and Shine, 1998). We have never observed *O. okinavensis* basking in the daytime at our study site. Furthermore, only filtered insolation and patchy spots of sunlight are available at our study site, negating the possibility that *O. okinavensis* can extensively increase its BT in retreat sites in the daytime. To clarify the thermoregulatory strategy of *O. okinavensis* it is necessary to investigate the preferred BT of the snake through laboratory experiments, the operative temperature in the habitat both at night and in the daytime, and the field BT of the snake in the daytime using temperature-sensitive radiotransmitters (Hertz et al., 1993).

We tested *O. okinavensis* for possible physiological adaptation to cool temperatures by hypothesizing that digestion of food at low temperatures is faster in *O. okinavensis* than in other species that are active at higher body temperatures. Table 3 summarizes the literature records on the duration of digestion in snakes in relation to the ambient temperature. At ambient temperatures between 10 and 20°C, the rate of digestion is from 60 to 336 h. Although many factors, such as prey type and relative body mass, affect the duration of digestion (Henderson, 1970; Skoczylas, 1970; Naulleau, 1983b), it is unlikely that *O. okinavensis* has the ability to digest food faster than other snakes (see Lillywhite et al., this volume). On the other hand, at lower temperatures such as between 10 and 15°C, most snakes do not digest food completely and eventually regurgitate (Table 3). In the present experiment, two of six *O. okinavensis* regurgitated frogs within 24 h after feeding. We do not, however, consider this a physiological reaction associated with low temperatures because in other snakes regurgitation can occur several days after feeding (Naulleau, 1983b; Stevenson et al., 1985; Dorcas et al., 1997). Rather, we highly suspect that regurgitation in male *O. okinavensis* was a reaction caused from forced-feeding. We, therefore, suggest that *O. okinavensis* is capable of retaining stomach contents for longer periods for digestion at low temperatures.

The venom of the Western Diamond-backed Rattlesnake (*Crotalus atrox*) is known to facilitate the digestion of prey, and the effect of the venom is more pronounced when digestion proceeds at 15°C than at 25°C (Thomas and Pough, 1979). The toxicity of *O. okinavensis* venom is relatively low (Toriba and Sawai, 1990), and this snake usually swallows prey animals alive (Koba, 1962; A. Mori, unpublished). Thus, it is probable that the venom of *O. okinavensis* also facilitates the digestion of prey, especially at low temperatures.

Gregory (1982) suggested that reptiles that evolved in temperate zones are likely to remain active at temperatures too cold for species that evolved in

Table 2. Literature records of body temperatures (BT) of viperid snakes. Data obtained during hibernation excluded.

Taxon	Activity[1]	Study site or locality	Latitude[2]	Mean BT[3]	Range BT[4]	Reference
Agkistrodon contortrix	d, n	Lawrence, Kansas, USA	39		17.5–34.5	Fitch, 1956
		Lawrence, Kansas, USA	39		14–34	Fitch, 1960
		Shelby, Tennessee, USA	35–36	23.9–27.1		Sanders and Jacob, 1981
A. c. mokasen	d, n	North America	34–52	27	17.5–34.5	Brattstrom, 1965
A. piscivorus	d, n	Western Texas, USA	26–35	26.2	24.6–27.7	Brattstrom, 1965
		Levy, Florida, USA	29		6–33	Wharton, 1969
A. p. piscivorus		Hopewell, Virginia, USA	37	26.1[5]		Blem and Blem, 1990
		Camden, Georgia, USA	31	25.7	21–35	Bothner, 1973
Calloselasma rhodostoma	n	Kedah State, West Malaysia	6	27.0–27.2		Daltry et al., 1998
Crotalus atrox	d, n	Riverside, California, USA	34		18–?	Cowles and Bogert, 1944
		North America	20–37	27.4	21.0–34.0	Brattstrom, 1965
		Sonoran Desert, Arizona, USA	32–34	29.3		Beck, 1995
C. cerastes	d, n	Riverside, California, USA	34	31.4	17.5–?	Cowles and Bogert, 1944
		North America	28–38	26.2	20.6–33.5	Brattstrom, 1965
		San Bernardino, California, USA	34	25.3	8.2–38.1	Secor and Nagy, 1994
		Mojave Desert, California, USA	34	26.3–28.3	15.7–38.1	Secor, 1995
C. c. cerastes		Southern California, USA	34–38	25.5	14.8–37.0	Cunningham, 1966
C. c. laterorepens		Palm Desert, California, USA	34	25.8[5]	13.6–40.8	Moore, 1978
C. horridus	d, n	Northeastern Kansas, USA	39		21.2–31.7	Fitch, 1956
		North America	25–45	25.9	21.2–31.7	Brattstrom, 1965
		Warren, New York, USA	43–44	26.9	12.5–33.3	Brown et al., 1982
C. lepidus	d	Boquillas, Texas, USA	29	29.9	21.5–35.5	Beaupre, 1995
		Grapevine, Texas, USA	33	28.8	17.4–38	Beaupre, 1995
C. mitchellii pyrrhus	d, n	North America	28–35	30.3	26.3–31.8	Brattstrom, 1965
		Palm Desert, California, USA	34	31.2[5]	18.8–39.3	Moore, 1978
C. molossus	c, d, n	Sonoran Desert, Arizona, USA	32–34	29.6		Beck, 1995
C. pricei	d	North America	22–32	21.1	18.0–23.8	Brattstrom, 1965
C. ruber	d, n	Riverside, California, USA	34	24.0 (24.0[5])		Brattstrom, 1965
C. scutulatus	d, n	North America	18–38	30.0	22.2–34.0	Brattstrom, 1965
C. tigris	c, d, n	Sonoran Desert, Arizona, USA	32–34	29.5		Beck, 1995
C. viridis	c, d, n	British Columbia, Canada	50	30–35	11.9–37.8	Charland and Gregory, 1990
		Southwestern Idaho, USA	42–47	28.4		Diller and Wallace, 1996
C. v. helleri		Southern California, USA	33–37	28.9	21.0–33.4	Brattstrom, 1965
		Los Angeles, California, USA	33–35	29.4[5]	27.6–30.8	Brattstrom, 1965

		Southern California, USA	33–37	25.4	9.3–37.8	Cunningham, 1966
C. v. lutosus		Northwestern Utah, USA	40–42	26–30	16–35	Hirth and King, 1969
C. v. oreganus		Washington, USA	46–49	24.5	13.5–33.5	Vitt, 1974
C. v. viridis		Carbon, Wyoming, USA	41–43	26.5	5–36	Graves and Duvall, 1993
C. willardi	d	North America	23–32	30		Brattstrom, 1965
Echis carinatus	n	Shagu, Iran	27	37.5		Anderson, 1963
		Tamil Nadu, India	10	30[5]		Aruna Devaraj and Rajendran, 1988
E. coloratus	c	Riyadh, Saudi Arabia	25	27.6–30.7	21–36	Al-Johany and Al-Sadoon, 1996
Gloydius blomhoffii	d, n	Tsukuba, Ibaraki, Japan	37	27.8	20–35	Kadowaki, 1996
G. brevicaudus	d, n	Zhejiang, China	26–32		20–39	Wang et al., 1983
		Zhejiang, China	26–32		20–30	Cao et al., 1988
Vipera aspis	d, n	France?	37–51	29	11–37	Saint Girons and Saint Girons, 1956
		Central-Pyrénées, France	43–44	27–29	11–30	Duguy, 1972
		Central-Pyrénées, France	43–47	30.9–32.7[5]		Saint Girons, 1978
		France?	37–51	30.5–31.6[5]		Naulleau, 1979
		France?	37–51	31–33[5]		Naulleau, 1983b
V. a. aspis		France?	37–51	31.5–32.7[5]		Saint Girons, 1975
V. ammodytes	d, n	Southeastern Europe	38–48	30.8–32.5[5]		Saint Girons, 1975
		Southeastern Europe	38–48	29.8–33.2[5]		Saint Girons, 1978
V. berus	d	France?	44–69	26.5	10–34	Saint Girons and Saint Girons, 1956
		Western Europe	44–69	30.0	20–38	Spellerberg, 1976
		Massif central, France	45–47	31.0–33.6[5]		Saint Girons, 1978
		Britain?	50–58	33.2		Gaywood and Spellerberg, 1996
V. b. berus		France?	44–69	31.3–32.5[5]		Saint Girons, 1975
V. dinniki	d	Sochi, Caucasus, Russia	53	26.7–28.5	20.2–35.1	Tuniyev and Volcik, 1995
V. latastei	d	Iberian Peninsula?	36–44	27.5	6–38	Saint Girons and Saint Girons, 1956
		Sierra Nevada, Zara, Spain	37, 41–42	31.2–32.5[5]		Saint Girons, 1978
V. seoanei	d	France?	42–44	31.4–32.6[5]		Saint Girons, 1975
		Pyrénée-Atlantiques, France	43	30.5–33.0[5]		Saint Girons, 1978
V. ursinii	d	France?	40–60?	28	11–38	Saint Girons and Saint Girons, 1956
		Mt. Lures, France	44	30.0–33.2[5]		Saint Girons, 1978
V. ursinii rakosiensis	d	Central Hungary	47		15–35	Újvári and Korsós, 1997

[1]Data from various published sources. When activity time varied seasonally or geographically, all possible times are indicated. Noted activity time does not necessarily correspond to time of day when the BT was measured; c = crepuscular; d = diurnal; n = nocturnal. [2]Approximate latitudes of the field study sites or localities of animals used for laboratory experiments are indicated. When these data were unavailable, the latitudinal range of the distribution is noted. [3]Mean values of active body temperatures obtained in nature or semi-natural enclosures. [4]Range of body temperatures during activity. [5]Mean values of preferred body temperatures measured in a laboratory thermal gradient.

Table 3. Literature records of temperature and rate of digestion in snakes. Data presented were obtained only at temperatures between 10°C and 25°C. Digestion rate: DR 1 = duration from feeding until no stomach contents were visible on X-ray photographs. DR 2 = duration from feeding to first excretion.

Species (Reference)	Prey	Relative mass of prey (%)	Ambient temperature (°C)	DR 1 (h)	DR 2 (h)	Occurrence of regurgitation (%)
Boidae						
Charina bottae	Mice	10–15	10	Not digested		100
(Dorcas et al., 1997)			15	240[1]		No
			20	108[1]		No
			25	70[1]		No
Colubridae						
Diadophis punctatus arnyi	Earthworms	?	15–25		72-336	No
(Henderson, 1970)						
Elaphe guttata guttata	Mice	10–25	18		180	No
(Greenwald and Kanter, 1979)			20		132	No
Natrix maura	Fish	~ 10	10		Not digested	100
(Hailey and Davies, 1987)			15		~ 96	20
			20		~ 60	No
			25		~ 31	No
N. natrix	Frogs	20–25	5	Not digested		No
(Skoczylas, 1970)			15	Not digested		Yes
			25	60		No
Thamnophis elegans	Mice	5–22	10	Not digested		100
(Stevenson et al., 1985)			15	~ 192[1]		33.3
			20	~ 134[1]		No
			25	~ 58[1]		No
Viperidae						
Ovophis okinavensis	Frogs	13–31	10–24	214–376 <		33.3
(this study)						
Vipera aspis	Mice	~ 10	10		Not digested	100
(Naulleau, 1982, 1983a)			15		253	55.8
			20		126	7.7
			25		76	7.4
V. ammodytes	Mice	~ 10	15		307	70.2
(Naulleau, 1983b)			20		153	< 10
			25		104	< 10
V. berus	Mice	~ 10	10		Not digested	100
(Naulleau, 1982, 1983b)			15		173	< 33.3
			20		82	No
			25		63	No
V. kaznakovi	Mice	~ 10	15		241	75
(Naulleau, 1983b)			20		104	No
			25		97	No
V. latastei	Mice	~ 10	15		220	—
(Naulleau, 1982, 1983b)			20		189	< 10
			25		122	< 10
V. seoanei	Mice	~ 10	15		Not digested	100
(Naulleau, 1982, 1983b)			20		118	< 11.3
			25		91	< 11.3

[1]Values calculated from figures in references.

subtropical and tropical zones. However, because other congeners, as well as most members of other Old World crotaline genera exclusive of *Gloydius*, are nocturnal and are distributed in subtropical and tropical regions of Asia (Gopalakrishnakone and Chou, 1990; Golay et al., 1993), it is likely that *O. okinavensis* was derived from a tropical, nocturnal species through an adaptation to low temperatures. *Ovophis okinavensis* appears to be an example of a snake adapted to cool environments in the subtropics, where neither latitude nor elevation is high. We hypothesize that the high activity of *O. okinavensis* at low body temperatures may have evolved to exploit a rich but temporally restricted food resource (i.e., frogs that aggregate for breeding in winter). To test this hypothesis, the foraging activity of *O. okinavensis* in areas where no such frogs occur should be examined (Moriguchi, 1989). Activity and thermal characteristics of *O. okinavensis* in summer should be also studied in detail to elucidate the extent to which this species depends on winter foraging and is adapted to low temperatures.

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