

Nest Attendance by a Female Malayan Pit Viper (*Calloselasma rhodostoma*) in Northeast Thailand

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ABSTRACT.— The function of egg attendance in pit vipers is understudied and poorly understood. Temperature sensitive radio telemetry was used to study nesting behavior and body temperature in a free ranging, female *Calloselasma rhodostoma*, which laid and attended a clutch of three eggs at a location in northeast Thailand. Oviposition occurred between 11 and 24 August, 2004 and all eggs had hatched by October 12, 2004 (incubation period = 49-62 days). The small clutch size was probably due to small maternal body size. The nest site was a rock crevice on a rocky, north facing slope, in mature deciduous dipterocarp forest. The female apparently remained coiled around the eggs for the entire incubation period with an average body temperature (T_b) of 27.1 °C (SD=1.61, range 23.7 to 30.4, $n=60$). Maternal T_b was slightly higher (1.5 °C) than that of an operative temperature model in a similar, nearby microhabitat, suggesting an occurrence of a small amount of maternal thermogenesis. The female fed once during incubation and underwent ecdysis at or near the time the eggs hatched. Little parental care was observed beyond the time of hatching.

KEY WORDS: nest attendance, pit viper, nest site, clutch size, body temperature, parental care

INTRODUCTION

The Malayan Pit Viper (*Calloselasma*

rhodostoma) is a tropical pit viper which occurs in western Laos, southern Vietnam, Cambodia, West Malaysia, Java, and most of Thailand (Gloyd and Conant, 1990; Orlov et al., 2002). *Calloselasma rhodostoma* is oviparous and one of a minority of snakes that provides parental care to offspring in the form of egg attendance (York and Burghardt, 1988; Gloyd and Conant, 1990). Little is known about the ecology of *C. rhodostoma* in general and most data on nesting behaviour in this species come from the laboratory. No detailed studies of nesting

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behaviour of free ranging *C. rhodostoma*, or other nest attending vipers, have been conducted to date and the function, costs, and benefits of this behavior are poorly understood (Shine, 1988).

Parental care is uncommon in reptiles but does occur in a variety of lizards, snakes, and crocodylians (Shine, 1988). Parental care occurs in only about 2% of oviparous squamates and has been reported in 58 snake species from 33 genera. The most common form of parental care in snakes is "nest attendance" in which the female remains with the eggs after oviposition (Shine, 1988). In some snakes the parent merely remains near the eggs but in others the maternal female coils tightly around the eggs. Nest attendance presumably functions in protection of the eggs but active defence of a nest has rarely been observed and the terms "nest guarding" or "egg-guarding" should only be applied to situations where active defence of the nest or eggs has been confirmed through field observation. Several species of the genus *Python* coil about the eggs and raise the temperature of the clutch above ambient through shivering thermogenesis (Harlow and Grigg, 1984; Shine 1988). This phenomenon, termed "egg brooding", is only documented in pythons but the possibility of egg brooding occurring in other species of snakes has rarely been tested (Shine, 1988). Some viviparous snakes also show parental care for the young after parturition (Shine, 1988; Greene et al., 2002). Parental care after parturition appears widespread among viviparous viperids but it is not known if post-hatching parental care is provided to hatchlings in oviparous species (reviewed in Greene et al., 2002).

Twelve viperid species are reported to remain with their eggs during incubation (Shine, 1988). Female *C. rhodostoma*, and at least six other oviparous, old world pit vipers, coil closely around their eggs during incubation in a behavior very similar to that of egg brooding pythons (Gloyd and Conant, 1990; Greene et al. 2002). Because the behavior of coiling about the eggs in *C. rhodostoma* is so similar to that of egg brooding pythons, the possibility of

thermogenesis occurring during egg attendance should be investigated. Herein, we report observations of parental care and body temperature during nest attendance in a free ranging female *C. rhodostoma*.

MATERIALS AND METHODS

Study area

The study was conducted at the Sakaerat Environmental Research Station (SERS), a 78 hectare wildlife preserve in Nakhon Rachasima Province, in northeast Thailand. Habitats at SERS include deciduous dipterocarp forest (DDF), dry evergreen forest (DEF), and abandoned agricultural areas (see Inger and Colwell, 1977).

Radio tracking

The study animal was captured opportunistically near the SERS compound, measured for snout-vent length (SVL) and total length (TL) using a squeeze box (Quinn and Jones, 1974), and weighed ± 0.1 g using a triple beam balance. Sex was determined by probing and external morphology (Gregory, 1983; Schaefer, 1934). The study organism was surgically implanted with a 3.8 g, temperature sensitive, radio telemeter (Holohil Systems Ltd., Carp, Ontario, Canada, Model PD-2T) according to methods outlined in Reinert and Cundall (1982). Before implantation the transmitter was calibrated in a water bath over the range of temperatures the snake was likely to encounter in the environment (10 to 40°C at ca. 5° increments). Calibration curves explained 98.8% of the variance in transmitter temperature. The snake was held for 2 days and released at the point of capture. A Wildlife Materials TRX 1000 receiver with a Yagi three-element directional antenna was used to locate the study animal most days during the course of the study although there are several 3 or 4 day gaps during which field work was temporarily suspended. Multiple locations were made on many days. We attempted to minimize disturbance to the snake during radio tracking.

Snake locations (UTM grid system) were determined using a GPS unit and distances between locations were calculated using simple planar geometry.

The area within 50 m from the nest site was intensively searched by two people on September 3, 2004 for the presence of other *C. rhodostoma* to determine if communal nesting or biparental care was occurring. The area was frequently searched less intensively throughout the course of the study.

Temperature determinations

Each time the snake was relocated air temperature (T_{air}) at approximately 1 m above the snake was determined using a mercury bulb thermometer. Substrate temperature (T_{sub}) was also obtained from a shaded spot within 1 m of the snake using a flat bulb mercury bulb thermometer. The transmitter inter-pulse interval (IPI) was determined using stop watch or pulse interval timer for later calculation of the snake body temperature (T_{b}). In order to determine the likely T_{b} of a snake not exhibiting thermogenesis, in a habitat similar to the nest site, we also recorded temperature of an operative temperature model (T_{op} , Bakken, 1992) placed in a rock crevice near the nest site from 11 August to 9 September. The operative temperature model was constructed of copper tubing (2 cm diameter, 15 cm long) painted reddish brown to match the coloration of *C. rhodostoma* (Bakken, 1992). Tubing diameter was similar to diameter at mid-body of our study animal and tubing length was approximately the width of the coiled snake (Peterson et al., 1993). A Thermochron iButton (Dallas Semiconductors, Dallas, Texas, USA: see Angilletta and Krochmal, 2003), was wrapped in aluminium hardware cloth to prevent the Thermochron from making contact with the side of the tubing and placed inside the tube. The Thermochron recorded T_{op} once per hour.

Sometimes IPI was obtained remotely, without making observations on the snake or recording T_{sub} or T_{air} and on some occasions equipment failures made obtaining IPI data impossible. For these reasons there are unequal numbers of observations of T_{b} , T_{sub} , and T_{air} and

not all of these observations are paired. SERS staff recorded relative humidity daily at 0700 hours local time at five locations within the SERS.

Statistical analyses

Average snake T_{b} was compared to T_{op} , T_{sub} , and T_{air} . Scores of $T_{\text{b}}-T_{\text{op}}$, and $T_{\text{b}}-T_{\text{air}}$ were normally distributed based on a Shapiro-Wilke Test ($W=0.98$, $p=0.66$ and $W=0.972$, $p=0.64$, respectively) so a paired t -test was used to compare T_{b} with T_{op} and T_{air} . The T_{op} value from the time nearest to that of the T_{b} reading was used for comparison in the paired analyses. The scores of $T_{\text{b}}-T_{\text{sub}}$ were not normally distributed ($W=0.920$, $p=0.03$) so a Wilcoxon Signed Rank test was used to compare T_{b} with T_{sub} . Relative humidity values from all five locations during the incubation period were pooled for determination of means, variance, and ranges to give a general idea of the relative humidity levels at SERS. Statistical analyses were conducted using SAS version 9.1 for Windows.

RESULTS

The female study animal was captured on 19 May 2004. At the time of capture she weighed 79.2 g and was 478 mm in SVL, and 540 mm TL. The 3.8 g radio transmitter (4.8 % of the total body weight of the snake) was implanted on 20 May. The snake did not appear to be gravid during processing and surgery. There were no complications with the surgery and the snake appeared healthy and active when released at the point of capture on 22 May. Her movements after release appeared normal relative to six other radio tagged *C. rhodostoma* at the site.

On 11 July she moved to the vicinity of the location at which she would later oviposit, and remained there until 31 July, occupying three different locations. She occupied a location under a large, flat rock 4 m from the future nest site from 11 July until 28 July. Scratches in the earth surrounding the rock crevice were observed on 13 July and indicate a mammalian predator may have unsuccessfully attempted to predate the



FIGURE 1. Photograph of the rock crevice nest site of female *Calloselasma rhodostoma* at Sakaerat Environmental Research Station, Nakhon Rachasima Province.

study animal. She was observed approximately 50 meters away from the future nest site on 3 August and arrived at the actual nest site by 11 August. The presence of eggs was not confirmed until 24 August 2004 though oviposition may have occurred some time prior to this. The eggs were difficult to see because the snake was coiled around them. Clutch size was not determined with certainty until the eggs hatched and the hatchlings had left the nest.

The nest was located in a mature, deciduous dipterocarp forest, on a rocky, north facing slope (Fig. 1). The clutch was located in a crevice formed by two rocks which were leaning against each other forming an A-shaped cavity. The opening of the cavity was approximately 30 cm across at the bottom and 13 cm in height and was partially obstructed by dead twigs and leaf litter. The eggs were in contact with a dry soil substrate.

A total of 61 visual observations were made on the snake on 56 days during nest attendance. On every occasion the snake was coiled about the eggs. The extent to which the eggs were exposed varied slightly but the amount of egg

surface visible never exceeded approximately 20%. The snake's head was always oriented toward the opening of the crevice and the body position varied little from day to day.

One egg had hatched by 10 October 2004 and the hatchling snake was observed lying on the coiled mother. On the morning of 12 October the remaining two eggs had hatched and all the snakes had left the nest. Three egg shells remained in the nest and were collected. We were unable to find the hatchlings and the mother was found 58 m from the nest site.

The female was collected on 1 November for removal of the radio transmitter and post-radio tracking processing as the life expectancy of the radio transmitter battery was coming to an end. After defecation and removal of the radio transmitter on 21 November she weighed 83.0 g and measured 52.5 cm SVL and 59.0 cm TL. She had grown 3.8 g in weight, 4.7 cm in SVL, and 5.0 cm in TL over the 165 day radio tracking period.

Feeding and ecdysis

The female snake was observed with food lumps in her gut on 4 October, and 1 November. The 4 October observation was made towards the end of the incubation period. The 1 November observation was made after the eggs had hatched and she had moved away from the nest site. She had shed by October 12, very close to the time that the eggs hatched.

Body temperatures and environmental variables

The female had an average T_b of 27.1 °C (SD=1.62, range 23.7 to 30.4 °C, $n=60$) during the period of nest attendance. T_{air} averaged 28.0 °C (SD=1.9, range 25.0 to 32.8, $n=36$) while T_{sub} averaged 28.5 °C (SD=1.9, range 26.0 to 34.5, $n=38$). T_{op} under a rock in the vicinity of the nest site averaged 25.2 °C (SD=1.1, range 23.0 to 30.0, $n=880$).

T_b was an average of 1.5 °C warmer than simultaneous T_{op} based on a paired t -test ($t=11.82$, $p < 0.0001$, $n=46$). Average T_b was 1.8 °C cooler than simultaneous T_{air} ($t=-7.59$, $p < 0.0001$) and was also significantly cooler than simultaneous T_{sub} by 2.1 °C based on a Wilcoxon's Signed Rank test ($S=-232.5$, $p < 0.0001$). The maximum difference between our female's T_b and T_{op} was 3.4 °C. All the largest positive differences we observed between T_b and T_{op} occurred in the late afternoon and early evening when T_e was dropping. Relative humidity at SERS averaged 86.9% (SD=5.3, range 74 to 98, $n=460$) during the incubation period.

DISCUSSION

Timing of oviposition, hatching, and mating

Our data on one female support an August oviposition period and an October hatching time for *C. rhodostoma* at SERS in northeast Thailand. Mating was not observed. Male *C. rhodostoma* engage in combat rituals during mating (York, 1984) and this was not observed in any of the three males we radio tracked so mating may have preceded the initiation of our study.

The timing of reproductive activities of *C. rhodostoma* vary across the species range (Daltry, 1995; see Table 1). Apparently, mating is initiated by the start of rains, after a period of aestivation during the dry season (Gloyd and Conant, 1990). Rainy season starts in April or May in eastern Thailand, southern Laos, and Cambodia, in February or March in peninsular Thailand, and in October and November in Java (Daltry, 1995). Daltry (1995) reports that mating coincides with onset of the rainy season in each of the above mentioned areas, but little data exist on the subject (Table 1). Data on timing of oviposition and hatching also vary across the range of *C. rhodostoma* and no clear patterns are discernable (Table 1).

Our data on timing of reproduction differ from several other reports from Thai *C. rhodostoma* (Table 1). Most of these data come from captive snakes (eg. Chanhome, 1998; Chanhome et al. 2001; Werler, 1970) which may not reflect behavior in free ranging animals but Purananda (1957) reports that *C. rhodostoma* "north of Prachuap" oviposite in May while those in peninsular Thailand do so in August. *Calliseltis rhodostoma* in Laos (Deuve, 1970) are reported to oviposite in June and July which differs from the snakes at SERS. More data on timing of reproduction in *C. rhodostoma* across the range are needed.

Incubation period

The incubation period of 48 to 62 days observed for *C. rhodostoma* in this study is comparable to, but somewhat longer than, other reported incubation periods for the species (Table 1). Even the minimum possible incubation period for our observed clutch, 49 days, is still the longest reported for the species. The incubation period we observed may have been longer than those observed for captive clutches because environmental conditions in the laboratory may have been more favourable for development of the young. Our data may represent a more realistic estimate of incubation period for free ranging *C. rhodostoma* in northeast Thailand.

TABLE 1. . Summary of literature on reproductive biology of *Calotesasma rhodostoma*. Study type: F = field study, C = data from captive snake(s)

Locality	Time of Mating	Time of Ovipositing	Time of Hatching	Incubation Period (days)	Clutch size	Number of Clutches	Maternal Body Size	Study Type	Reference
NE Thailand		11 - 24 Aug.	10-12 Oct.	49-62	3	1	540mm SVL	F	Present Study
Southern and Central Thailand	April	June - July	Aug.	37-46	17-29	4		C	Chanhome et al., 2001
Thailand (Pitsanoluk?)		July -Aug.			27	1	802 mm SVL	C	York & Burghardt, 1988
Thailand		24-May	30-Jun	37	14	1		C	Werler, 1970
Thailand		1 Sept.		47	13	1		F	Smith, 1915
Thailand "north of Prachuap"		May	"beginning of rainy"	28	20-40	?		F?	Purananda, 1957
Peninsular Thailand		Aug.		"	"	?		F?	Purananda, 1957
Peninsular Thailand		Aug. 5		39-40	17	1		C	Chanhome, 1998
Peninsular Thailand			26-Jul		31	1	264 g	F	Bulian, 2003
Laos		Eggs collected			25-35	?		F	Deuve, 1970
W. Malaysia	Feb.-Mar.	June -July			?	?		F	Daltry, 1995
West Java		Feb.- Mar.			19-29	4	702-794 mm TL	F/C	Bergman, 1961
West Java			8-Jun		22	1		F	Kopstein, 1938
West Java	Oct.-Nov.							F	Daltry, 1995
?		Sept. 5	Oct. 13		22	1	773 mm TL	C	Gloyd & Conant, 1990

Clutch size

The clutch size of three observed in this study is by far the smallest reported for this species (Table 1). *Calloselasma rhodostoma* typically produce clutches of 17 to 40 eggs but all reports of clutch size which include maternal body size indicate maternal females were over 700 mm TL (Table 1). Our female was considerably smaller (79.2 g, 540 mm TL) than the snakes in all of the above accounts. For example a 264 g *C. rhodostoma* produced a clutch of 31 eggs in southern Thailand (Bulian, 2003). The relationship of female body size to clutch size has not been well studied for *C. rhodostoma* but the small clutch size observed in this study may be attributable to small maternal body size. Brood size is generally correlated to female body size within each snake species although exceptions to this trend exist (Shine, 1977; Fitch, 1970). The smallest gravid female *C. rhodostoma* found in a study in Jakarta was 648 mm SVL (Bergman, 1961). Gloyd and Conant (1990) consider *C. rhodostoma* larger than 300 mm TL to be “non-juvenile” but they provide no justification for this. Bergman (1961) considered female *C. rhodostoma* to be adult at approximately 452 mm TL. *Calloselasma rhodostoma* at SERS appear to be somewhat smaller than those found further south in the species range (J. Hill, in preparation).

Nest site and benefits of nest attendance

Our study provides the first report of *C. rhodostoma* nesting in a rock crevice (Figure 1). Existing data on nesting locations are limited but *C. rhodostoma* appears to utilize a variety of microhabitats for nesting. *Calloselasma rhodostoma* generally nest above ground, in humid, shady spots, (but not saturated ground), including log piles, long grass, junk piles, and beneath houses (J. Daltry, pers. com.). *Calloselasma rhodostoma* in Laos nested in sheltered holes, often at the foot of banana trees, in sandy soil, covered with dry leaves, and exposed to the sun (Deuve, 1970). Three *C. rhodostoma* nests in southern Thailand were “positioned in fairly sheltered localities, but were not covered” (Leakey, 1969). Bulian (2003)

observed a *C. rhodostoma* in Surathani, Thailand nesting in an open area, on moist soil, in grass about 40 cm tall.

The rock crevice used by our female for nesting would clearly provide physical protection for the parent and the eggs and would also prevent visual detection of the clutch from the above. Raptors prey on *C. rhodostoma* at SERS (J. Hill, personal observation) and the rock crevice would provide protection against avian predators. The rock crevice nest site was probably easily defended by active means. Our study animal kept her head oriented in the direction of the crevice opening, making it difficult for an animal to predate the eggs without sustaining a bite from the venomous parent. Scratch marks on the ground at the opening to different rock crevice occupied by our female while she was gravid indicate that she may have survived an attack from a predator in a location very similar to the nest site. Pit vipers which coil around their eggs probably actively defend them when necessary and their nesting behavior is probably best described as “nest guarding” (Shine, 1988).

York and Burghardt (1988) assumed that *C. rhodostoma* laid eggs on the ground without cover and that the coiling female provided passive defence of the clutch by virtue of her camouflaged body. The benefit of protection of the clutch through crypsis would be limited for snakes nesting in such protected locations but might prevent visual detection of the clutch from a predator on the ground peering into the crevice. Protection of the clutch by crypsis is probably important for *C. rhodostoma* nesting in less sheltered areas.

Several reports exist for biparental care in pit vipers, in which the males attend to the eggs with females (Deuve, 1970; Manthey and Grossman, 1997). We searched the vicinity of the nest extensively and found no other snakes, so it is unlikely that biparental care took place. Previous reports of biparental care may be erroneous (Shine, 1988). Lack of conspecific females in the nest site vicinity indicates nesting was not communal in this instance. Communal

nesting occurs in a number of other crotalines (Greene et al., 2002).

Coiling around the clutch probably also serves to regulate the egg's exposure to moisture. Maternal coiling around the eggs in *Python regius* substantially decreased desiccation of the eggs relative to non-brooded eggs and maternally brooded neonates were larger, heavier, and had longer jaws than non-brooded neonates (Aubret et al. 2005). A captive, egg attending *C. rhodostoma* varied the degree to which the eggs were exposed in response to relative humidity levels with the maternal female often covering the eggs completely when the humidity levels dropped below 70% (York and Burghardt, 1988). This behavior was thought to regulate moisture level and turgidity of the eggs. We observed slight variation in the extent to which our female exposed her eggs but exposure never exceeded approximately 20%, even during rainfall. Egg exposure was difficult to quantify because we could not see the clutch from above. Relative humidity levels at SERS never dropped below 70% nesting.

Thermogenesis

Our female's T_b was slightly (1.5°C) but significantly higher than the temperature of an operative temperature model in a nearby, similar microhabitat and it is possible that some maternal thermogenesis was occurring. The comparison of the nesting female's T_b with T_{op} probably provides the best test of the hypothesis that shivering thermogenesis was occurring because the operative temperature model was in the same microhabitat as the parent snake. T_{air} and T_{sub} were likely to differ from environmental temperatures inside the rock crevice due exposure to sunlight and wind not present in the rock crevice. Though statistically significant, the small average difference between T_b and T_{op} is not compelling evidence to suggest that our female was generating body heat above ambient. Shivering thermogenesis in egg brooding *Python spilotes spilotes* raised T_b almost 7°C above ambient temperature (Harlow and Grigg, 1984). A female *Python molurus bivittatus* raised T_b an average of 6.2°C above ambient while brooding

a clutch of eggs (Van Mierop and Barnard, 1976). The small average difference between T_b and T_{op} could have been due to slight temperature variations between microhabitats but we cannot rule out the possibility of small amount of heat being generated by the coiling snake. T_b was probably cooler than both T_{air} and T_{sub} because all measurements of T_{sub} and T_{air} were taken during the day between 09:00 and 17:00 at which time temperatures in the rock crevice were probably cooler than ambient due to lack of exposure to sunlight.

Our conclusions regarding the occurrence of thermogenesis in nest attending female *C. rhodostoma* should be considered tentative because we only have observations on one individual. *Calloselasma rhodostoma* may lack sufficient muscle mass to generate appreciable heat through shivering. Shivering thermogenesis may be restricted to pythons because of their large size and muscle mass (Shine, 1988).

Costs of nest attendance

A potential cost of reproduction to female snakes would be an inability to feed during ovogenesis and/or incubation (Shine, 1988). Gravid and pregnant female reptiles often show a reduction or cessation of feeding relative to non-gravid females and males (Shine, 1980; Gregory et al. 1999). This generality appears true for gravid female *C. rhodostoma*. None of fifty gravid female *C. rhodostoma* specimens collected from throughout Southeast Asia had food in their guts and their stomachs and livers appeared reduced in size (Daltry et al., 1998a). Koch (1991) also reports *C. rhodostoma* cease to feed during ovogenesis. Our data concur with these observations as our snake did not appear to feed while gravid.

Our female clearly fed during nest attendance just prior to the hatching of the eggs. Little data exists regarding feeding during nest attendance but two other accounts exist in the literature indicating that captive, nest attending, female *C. rhodostoma* left their clutch to feed (Smith, 1915; Gloyd and Conant, 1990). Chanhom et al. (2001) indicated that captive, gravid *C. rhodostoma* do not feed until after

oviposition but did not specify whether or not they fed during nest attendance.

Our female study animal does not appear to have suffered from lack of nutrition due to reproductive activities as evidenced by growth in both SVL (5.0 cm) and weight (3.8 g) during the radio tracking period which ended only about two weeks after the eggs hatched. The growth observed for our gravid female is, however, lower than the average 33.5 g weight increase of 4 non-gravid *C. rhodostoma* from West Malaysia during a similar time period (Daltry et al. 1998b).

Some viviparous female pit vipers exhibit post-parturient parental care (Greene, 2002). Little parental care was observed after egg hatching in this study. Ecdysis of the maternal female may be associated with egg hatching in *C. rhodostoma*. Our study animal shed her skin at approximately the same time as the eggs hatched. Bulian (2003) also observed that a female *C. rhodostoma* in Surathani, southern Thailand began shedding simultaneously with the hatching of the eggs. Ecdysis appears to be associated with various reproductive activities in other crotalines. (Greene et al., 2002; Hill, 2003).

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