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## BROODING IN THE MALAYAN PIT VIPER, *CALLOSELASMA RHODOSTOMA*: TEMPERATURE, RELATIVE HUMIDITY, AND DEFENSIVE BEHAVIOUR

DANIEL S. YORK<sup>1,2</sup> AND GORDON M. BURGHARDT<sup>1</sup>

<sup>1</sup>Department of Psychology, Graduate Program in Life Sciences (Ethology), The University of Tennessee, Knoxville, TN 37996.

<sup>2</sup>Present Address: Division of Biological Sciences, The University of Michigan, Ann Arbor, Michigan 48109.

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### ABSTRACT

A female Malayan pit viper (*Calloselasma rhodostoma*) laid a clutch of 27 eggs and remained coiled atop them until hatching. Possible functions of brooding were evaluated; these include regulation of temperature, regulation of moisture, and protection. The brooding female was not found to regulate the clutch's temperature but was found to vary the degree of egg exposure in accordance with fluctuations in the level of relative humidity. Body-jerking movements could be elicited in the female while she was brooding but not while she was off the nest. Body-jerking was elicited by prodding with an inanimate object as well as from a conspecific, and it is felt that this behaviour could function to ward off a potential predator.

## INTRODUCTION

This is a report on brooding of eggs by a female Malayan pit viper (*Calloselasma rhodostoma*). To elucidate possible functions brooding might have in *C. rhodostoma*, we collected data on temperature and humidity within the snake's enclosure. In addition, we observed the effect of physical disturbances on the brooding female.

Egg brooding has been observed in the lizards *Eumeces* and *Ophisaurus* (Noble & Mason, 1933; Evans, 1959; Vinegar, 1968). In snakes, brooding has been reported for various elapids and several viperids (Noble, 1935), boids (Vinegar *et al.*, 1970), and in a few colubrids (Bellairs, 1970; Oliver, 1955). Functions of brooding that have been explored include: defense of the nest (Noble & Mason, 1933; Noble, 1935; Pope, 1935; Oliver, 1956), behavioural regulation of nest temperature (Vinegar, 1968; Oliver, 1955; Cogger & Holmes, 1960), and physiological regulation of nest temperature (Hutchison *et al.*, 1966; Vinegar *et al.*, 1970).

## MATERIALS AND METHODS

A large brooding female (snout-vent length: 802mm) was housed together with two smaller females in a 90 x 60 x 60cm wooden enclosure fitted with a glass top and front side. The inside of the enclosure included a cypress bark mulch substratum, three large rocks arranged to provide crevices, a bowl 'pool' for water, and plastic foliage. The cypress mulch provided a suitable substratum in which the snakes blended well due to their cryptically coloured patterns. The mulch also formed a suitable substratum for nesting.

The snakes were kept on a 12/12 reversed light-dark cycle. Three 25-watt red ceramic coated light bulbs used during the dark cycle provided acceptable illumination for both direct and video monitored observations. A 250-watt infra-red heat reflector situated 1m above and at a 45° angle to the enclosure was turned on for four hours each day during the 12 hour light cycle. This caused the temperature in the enclosure to vary between 23° and 29°C through a 24 hour cycle. Likewise, the humidity level was varied between 70 and 100 per cent R.H. through periodic watering of the mulch substratum as well as misting the inside of the enclosure.

In order to test the hypothesis that brooding has an effect on the temperature of the eggs, data on the egg, air, and substratum temperatures were collected. Temperature readings during brooding by the large female were obtained from 3 thermistors connected to a YSI Model 4002 switch box, which was in turn connected to a YSI telethermometer. Both the switch box and telethermometer were next to the outside of the enclosure. Temperature was recorded simultaneously from air, substratum, and clutch. Air temperature was obtained by a thermistor hanging 15cm above the brooding female. Substratum temperature was taken from a thermistor 10cm in front of the brooding female, and clutch temperature was recorded from a thermistor placed between the coils of the female and her eggs. Temperature was recorded for

26 consecutive days. Temperature was generally recorded during the dark cycle. In addition, temperatures were recorded at 15 minute intervals over a 24 hour period in order to obtain a continuous sampling of temperature changes through a complete day cycle.

Data on the brooding female's response to changing levels of humidity were obtained by an Abbeon Relative Humidity Indicator positioned 22cm directly above the female. A Sony black and white video camera in front of the enclosure was focused on the hygrometer; a second camera was suspended above the enclosure and was focused on the brooding female with the film plane parallel to the floor of the enclosure. The pictures from the two cameras were combined with a Sony Special-Effects-Generator. Twelve-hour continuous recordings were made on a Panasonic time-lapse surveillance video recorder during the dark cycle over a period of 8 days; egg exposure and humidity data were recorded from them. The data consisted of 189 egg exposure-humidity data comparisons made at one-half hour intervals. Egg exposure was determined by projecting the video image onto a 13.3cm diagonal black and white monitor screen divided into 3mm squares and counting the number of squares in which eggs were visible.

## RESULTS

### TEMPERATURE

Temperature means, standard deviations, and ranges overlapped. But a Friedman non-parametric test of differences between simultaneous temperature readings was significant ( $\chi^2 = 71.7$ , d.f. = 2,  $p < 0.001$ ). Paired t-tests also showed that the mean substratum temperature was significantly lower from that of both the mean clutch ( $t = 10.45$ , d.f. = 152,  $p < 0.001$ ) and air ( $t = 7.66$ , d.f. = 152,  $p < 0.001$ ) temperatures, but that the mean clutch temperature did not differ significantly from that of air ( $p < 0.05$ ).

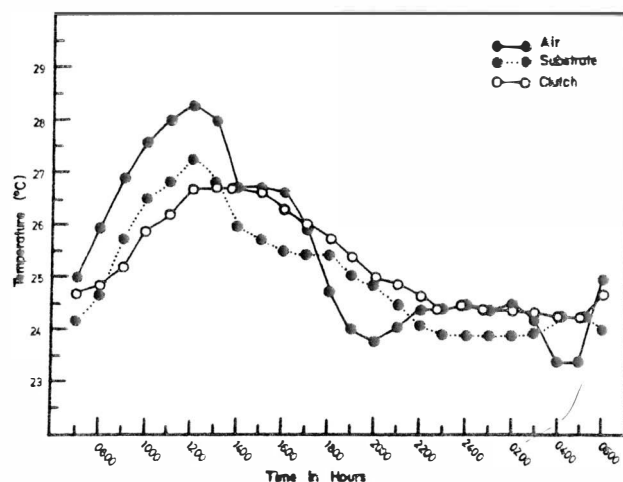


Fig. 1 Temperature changes over a 24 hour period during brooding in *Calloselasma rhodostoma*. Data points represent averages over 4 temperature readings taken at 15 minute intervals.

Fig. 1 shows changes in the temperatures of the substratum, clutch, and air over a 24 hour period. We obtained data points by averaging four consecutive temperature readings taken at 15 minute intervals from each thermistor.

#### HUMIDITY

We observed changes in the amount of eggs exposed occurring with changes in humidity. The female would often cover the eggs completely when the relative humidity decreased below 70 per cent. Spraying of the enclosure increased the relative humidity to 100 per cent. The female responded to the humidity rise with a loosening of her coils, thereby greatly increasing the amount of eggs exposed. On several occasions, relative humidity remained at or near 100 per cent for several hours. The female initially responded by loosening her coils but then decreased egg exposure by tightening them.

A plot of % R.H. and amount of egg exposure over time showed a consistent pattern of increased egg exposure following sharp rises in humidity. A 30 hour sample of this pattern is given in Fig. 2. High levels of egg exposure (egg exposure > 40) always lasted under two hours, regardless of % R.H.

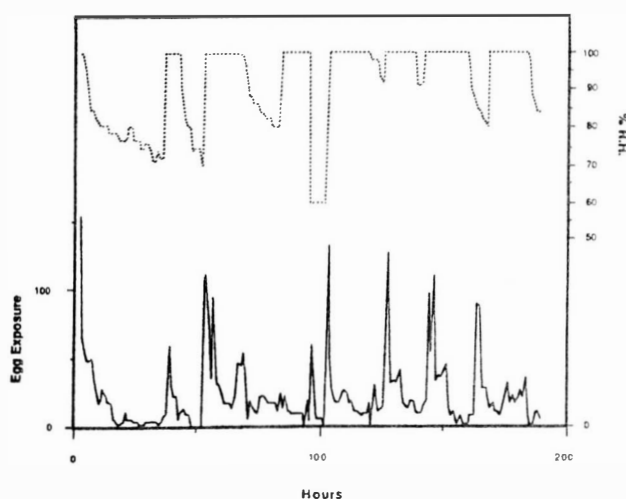


Fig. 2 One hundred and eighty hour sample of the amount of eggs exposed (see text) during brooding in *Calloselasma rhodostoma* (solid line) together with % R.H. (dashed line).

#### DEFENCE

We observed the brooding female to actively defend the nest by means of body-jerking. This behaviour was also observed by Matt Finstrom (unpublished manuscript) and appears to be similar to the 'body-jerking' of crotaline snakes in response to the presence of ophiophagous kingsnakes (Carpenter & Gillingham, 1975). In *Calloselasma rhodostoma*, body-jerking consisted of jabbing a short segment of the trunk against some intruding object and thereby forcing the object away from the snake. This response could be elicited by inanimate objects such as snake hooks as well as by conspecifics. Whenever body-jerking was directed against a conspecific, the latter initially reacted with a startle response, then froze for up to three minutes. During hatching, the female's body-jerking led to dispersion of the newly hatched

neonates. The body-jerking response disappeared two days after hatching of the neonates.

In one case the intruding conspecific was a gravid female who was very persistent in attempting to coil atop the already brooding female. We first observed these attempts on 3 September 1982, 27 days after the brooding female had laid her eggs. The non-brooding female was removed from the enclosure and was isolated in a small, separate terrarium. On 19 September 1982, the removed female laid eggs and coiled tightly around them. We lifted the second female off her nest so that the eggs could be weighed and measured, and she exhibited body-jerking to the snake hook as had the original female.

#### DISCUSSION

The temperature data do not indicate that brooding in *Calloselasma rhodostoma* has any effect on the subsequent temperature of the clutch except for decreasing the overall daily temperature variation. This temperature stabilising effect can be expected from any large covering body. Brooding female Indian pythons (*Python molurus bivittatus*) can maintain body temperatures as much as 7.3°C above either of the substratum or the ambient temperatures for extended periods (Hutchison *et al.*, 1966; Vinegar *et al.*, 1970). For the python, 33°C may be analogous to the 'lower critical temperature' of birds and mammals (Hutchison *et al.*, 1966); that is, the brooding animal only increases its rate of oxygen consumption once the ambient drops below 33°C.

The body temperature of the brooding female *Calloselasma rhodostoma* during the 24 hour sample was above ambient temperature for about 9 hours (see Fig. 1). This occurred during a steep decline in the air temperature after it had reached its peak at 0200 hours. During this period, the maximum temperature deviation between the air and clutch was only 1.4°C. It should be noted that as most temperature data were obtained during the cooler (dark) portion of the cycle, the bias was towards body temperatures warmer than ambient. Vinegar *et al.* (1970) suggest that the northerly distribution limit (circa 22° N. Lat.) of *Python reticulatus* was determined by the fact that it did not incubate its eggs; whereas *P. molurus* with its ability to increase its body temperature during brooding allowed it to extend its range into southern China (circa 27° N. Lat.). In contrast, the range of *Calloselasma rhodostoma* probably does not extend much further than Phitsanulok, Thailand (16.5° N. Lat.); a range which is more comparable to that of *P. reticulatus*. The mean temperature of a ten year period for the northerly part of *C. rhodostoma*'s range is 28.3°C during the period most likely for laying (World Weather Records 1950-60, Vol. 4, Asia). Bellairs (1970) mentions the possibility that brooding might protect reptilian eggs from chilling breezes, though the forested habitat of *C. rhodostoma* would lessen any such effect.

The calcareous shell of oviparous reptiles is an important adaptation associated with terrestrial reproduction (Spellerberg, 1982). The albumen layer

in *Amphibolurus b. barbatus* eggs reduces desiccation (Badham, 1971), however, humidity and moisture content of the surrounding substratum remain important factors in embryonic survival (Fitch & Fitch, 1967). Adaptation to the problem of desiccation of the porously membraned eggs is seen in the habit of some terrapins of moistening the nest with urine. The European terrapin (*Emys orbicularis*) drinks water when laying during hot weather thus replenishing her cloacal bladders with fluid which is used in moistening her nest and eggs (Bellairs, 1970).

Joshi (1967) showed the importance of humidity in the development of *Python sebae* eggs. He divided a single clutch into various groups and found that the groups kept at 65 to 80 per cent R.H. hatched, whereas the group kept below 40 per cent R.H. failed to hatch. A group kept in moist soil but in a dry and sunny place also failed to hatch.

Humidity may be only one of the factors determining egg exposure. Another factor might be egg turgidity, which might in turn be affected by humidity. In such a case, we postulate the following three sequences determining egg exposure: 1. Humidity high, egg turgidity low: expose eggs. 2. Humidity low, egg turgidity high (from excessive ground moisture): expose eggs. 3. Humidity low, egg turgidity low (or decreasing): cover eggs. In southeast Asia, where humidity levels are generally high, especially in forested areas, regulation of moisture might be more crucial than temperature regulation to the survival of the developing eggs. Deviations in precipitation level could have serious consequences on egg survival as eggs are laid during the period of greatest rainfall (Fig. 3).

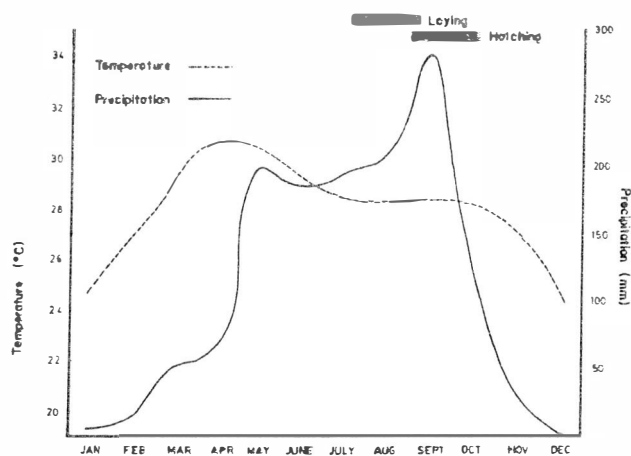


Fig. 3 Temperature and precipitation averages for a 10 year period at the Phitanulok, Thailand, weather station (16.50 N. Lat.) and approximate egg laying and hatching times for *Calloselasma rhodostoma*. (Weather information obtained from the U.S. Dept. Commerce, Environmental Sci. Services Admin., Environmental Data Service, World Weather Records 1950-60, Vol. 4, Asia.)

It is assumed that brooding in snakes serves to protect the eggs from predators, although the literature contains little direct evidence for this hypothesis. Oliver (1956) concluded that brooding in *Ophiophagus hannah* must be providing protection

since he found the female to be more concerned with covering the eggs (humidity maintenance?) than in driving off a potential predator. Noble (1935), after determining that certain female lizards that brood their eggs will actively defend them from predatory attacks, concluded that the same must be true for the majority of brooding snakes, as it would enhance their offsprings' survival with or without physiological thermoregulation.

Finally, it should be noted that brooding in *Calloselasma rhodostoma* can lead to passive defence provided by the camouflaging colouration of the brooding female. As the highly reflective white eggs are laid on top of the substratum floor, they would be very visible to a predator, but once covered by the brooding female they disappear under her body, whose colour and patterns blend in well with the ground.

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## HERPETOFAUNA OF THE LATE DEVENSIAN/EARLY FLANDRIAN COW CAVE SITE, CHUDLEIGH, DEVON

J. ALAN HOLMAN

Michigan State University Museum, East Lansing, Michigan 48824-1045 U.S.A.

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### ABSTRACT

The late Devensian/early Flandrian Cow Cave Site, Chudleigh, Devon, yielded a herpetofauna consisting of *Bufo bufo*, *Bufo calamita*, *Rana temporaria*, *Anguis fragilis*, and *Vipera berus*. This is a depauperate 'Rana-Bufo' fossil assemblage with *Rana* comprising 20 per cent and *Bufo* 77 per cent of the fauna. The endangered species *Bufo calamita* is reported for the first time as a fossil from Devon and for the second time only as a British fossil.

### INTRODUCTION

Other than a recent report on the Ightham Fissures, Sevenoaks Area, Kent (Holman, 1985) and Stuart (1979) on *Emys orbicularis*, the late Devensian and Flandrian herpetofauna of Britain has largely been neglected since the late 19th Century (Newton, 1879, 1894; Woodward, 1880). Nevertheless, a knowledge of late Pleistocene British herptiles is essential for the interpretation of their biotic responses to late Pleistocene environmental oscillations. Recently, through the kindness of Dr. Angela Milner of the British Museum (Natural History), I was allowed the privilege of studying the late Devensian/early Flandrian herpetofauna of Cow Cave, Chudleigh, Devon. The fossil herpetofauna of this site forms the subject of the present paper.

### THE DEVENSIAN AND FLANDRIAN STAGES

The Devensian is the last cold stage of the Pleistocene in Britain, and is thought to have begun about 110,000 years before the present (b.p.), and to

have lasted about 100,000 years (Stuart, 1982). The Flandrian is that period of time in Britain that began about 10,000 radiocarbon years b.p., equivalent to the Holocene on a world-wide basis. Sutcliffe (1985, p.61) provides a chart that indicates terminology of Flandrian equivalents in different parts of the World. Quite important events that occurred in the Flandrian and strongly influenced the British herpetofauna include (1) British isolation from the European Continent early in the stage, (2) extinction of several large mammals through hunting and habitat changes by humans, and (3) later introduction of exotic species and further modifications of the environment of the native species.

The ecological history of the Flandrian, based on pollen, mollusc and beetle studies, indicates a change from Tundra about 10,000 b.p. to a rapid warming to a climate as warm as today in southern England by 9,500 b.p. The birch community was replaced by hazel scrub between 8,700 to 8,100 b.p.; then a hazel and pine mixture about 8,100 to 7,100 b.p.; and finally deciduous forest from 7,100 to 5,000 b.p. (Coope, 1977;