To the Graduate Council:

I am submitting herewith a thesis written by Daniel Scott York entitled "Agonistic and Reproductive Behaviors in the Malayan Pit Viper (*Calloselasma rhodostoma*)." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Life Sciences.

Gordon M. Burghardt
G. M. Burghardt, Major Professor

We have read this thesis and recommend its acceptance:

Accepted for the Council:

Lawrence Minkel
The Graduate School

AGONISTIC AND REPRODUCTIVE BEHAVIORS IN THE MALAYAN PIT VIPER (*CALLOSELASMA RHODOSTOMA*)

A Thesis

Presented for the

Master of Science

Degree

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Daniel Scott York

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ABSTRACT

Agonistic and reproductive behaviors in the Malayan pit viper (*Calloselasma rhodostoma*) were investigated and found to occur mainly during the scotophase. Techniques developed to conduct observations on the snakes during the active part of their daily cycle permitted the development of an ethogram and documentation of male combat, courtship, mating and brooding behavior.

Male combat was observed and videorecorded on 10 occasions. An ethogram was constructed for use in analyzing combat. Associations between the various behavioral categories were analyzed through the use of a unique high efficiency computer routine which generates and maximizes resolution of data in a sociomatric matrix. Functions of male combat in the Malayan pit viper are discussed with an emphasis on reasons as to why males of this species apparently do not obtain sizes greater than that of females. From this discussion, it is felt that a large clutch size and annual breeding cycle is having a stronger positive effect on size in females than combat is having in males.

Courtship and mating were observed and are described. Subsequent laying and brooding of the eggs by the female Malayan pit viper was videotaped. Possible functions that brooding might be playing were examined; these included regulation of heat, regulation of moisture the clutch received, and protection. No effect on clutch temperature due to brooding was found; however, the brooding female was found to adjust the amount of clutch exposure to accommodate different

levels of relative humidity. During the period of brooding, the female would respond to conspecific or experimental perturbations by means of "body-jerking;" a behavior interpreted as defensive.

The video techniques developed for observations in the dark may have great use in dealing with similar problems in other species. Still, I found the Malayan pit viper to be an excellent representative species for investigations of the activities of nocturnal, crotaline snakes in a laboratory setting.

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CHAPTER I

INTRODUCTION

I. GENERAL GOAL OF THESIS

Ethology is a field of study which has frequently a strong reliance on the researcher's ability to make accurate observations of ongoing behaviors. As humans, we are visually oriented. The effect of this on ethology has been a predominance of studies on animals that are diurnal. The activities of many nocturnal animals have, to a large extent, gone on unseen behind a veil of darkness. Those nocturnal creatures living under the branches of a thick forest present an added hindrance to the would-be naturalist interested in bringing to light the activities engaged in by these animals in order to survive. Such an animal is the Malayan pit viper, *Calloselasma rhodostoma* (Viperidae, Crotalinae).

While I do not propose to solve these problems as they exist in the field, I do hope to present various techniques that may be used in a laboratory setting to overcome such problems. From the application of these methods, I have found the Malayan pit viper to be quite an active subject during its dark photophase. In this thesis I shall present a general description of agonistic and reproductive behaviors that I have observed and recorded over 18 months of observations. Furthermore, I shall present evidence on the role brooding plays in the regulation of moisture the clutch receives. I also hope to show that, through the use of proper techniques, the Malayan pit viper can be a

useful representative species for laboratory studies on the nocturnal behavior of crotaline snakes.

II. TAXONOMY

The Malayan pit viper belongs to the Crotalinae, one of the two major subfamilies of the Viperidae, which are those snakes possessing folding front fangs used in venom injection. Besides the Crotalinae (rattlesnakes and moccasins), the Viperidae also include the Viperinae (adders and true vipers). The most distinguishing feature between the two subfamilies is the presence of a thermally sensitive pit-organ in the Crotalinae. Boulenger (1896) included the Malayan pit viper in the crotaline genus *Agkistrodon*. According to gross external morphology (the presence of large head scales and absence of rattles) this placement appears correct. However, in 1957 S. A. Chernov successfully argued for a change in the Malayan pit viper's classification from *Agkistrodon rhodostoma* to *Calloselasma rhodostoma*, which is the name given to it by Cope (1895). Today the Malayan pit viper remains the single species of that genus.

The strongest part of Chernov's argument dealt with comparisons of cranial osteology among the *Agkistrodon*. He found the skull of the Malayan pit viper to be differentiated from all the skulls of other taxa at his disposal. In addition to the osteological differences, he listed the presence of smooth scales and oviparity as two further differentiating characteristics. Although the long-nosed viper (*A. acutus*) is also known to be oviparous (Pope, 1935), I am in general

agreement with Chernov in assigning the Malayan pit viper to a separate genus, and it shall be here referred to as *Calloselasma rhodostoma*.

III. GEOGRAPHY—HABITAT

Calloselasma rhodostoma is a Southeast Asian crotaline. Its reported range is Thailand (except for the north-east), Cambodia, the southern portion of Viet Nam, and the Malaysian subregion including Sumatra and Java (Smith, 1943; Taylor, 1965; Tweedie, 1953). According to Smith (1943) there is a specimen in the Natural History Museum, Paris, which is said to have come from Tonkin, which would considerably increase its range to the northeast.

Calloselasma rhodostoma is apparently common throughout its range, especially in low lying wooded areas near the coast (Smith, 1943). Still it has been found as high as 5000 ft on Mount Willis, Java (Boulenger, 1896). Tweedie (1953) felt that a climate with a more or less marked wet and dry season is essential. In a description by Hoesel (1959) it was noted as being nocturnal and thus not a lively captive for this reason. Its diet, according to Hoesel, consists of small mammals, birds and frogs. In the Reptile Behavior Laboratory at The University of Tennessee, neonates were fed regularly on small *Anolis* lizards and so it is assumed that in the field, at least the neonates would feed on small lizards and possibly other reptiles as well.

CHAPTER II

METHODS

I. SUBJECTS

The Malayan pit vipers used in this study were all captive bred. They included an adult female (No. 1) and an adult male (No. 2) hatched prior to 1979, two female littermates (Nos. 3 & 4) hatched in August 1980, two male littermates (Nos. 5 & 6) hatched in November 1978. The subjects were received from Mathew Finstrom's private collection, at the end of December 1981. The two females (Nos. 3 & 4) are the progeny of a mating between Nos. 1 & 2. Between 3 and 4 October 1982 fifteen males and seven females were hatched from a clutch laid by No. 1. The male (No. 2) died on 13 May 1982 during a feeding conflict with No. 1. The sizes and weights of these snakes are summarized in Tables 1 and 2.

When the subjects were housed together there was a problem with identification. Several methods were used to distinguish the snakes with varying success. The female No. 1 and male No. 2 could be identified according to size alone as both were notably larger than any of the others, and No. 1 was considerably larger than No. 2. The identification of the other four individuals was more difficult. Although there did appear to be slight color variations among the subjects, this proved to be of little help in identification as the color tone or hue in any one individual was subject to change as the

Table 1. Sizes of adult *Calloselasma rhodostoma* subjects used in the study. Measurements taken 18.08.83.

Subject	Sex	SVL (mm)	Total (mm)	Weight (g)
No. 1	F	802	895	428.8
No. 2*	M	595	717	229.0
No. 3	F	650	728	302.0
No. 4	F	594	668	162.1
No. 5	M	690	825	218.1
No. 6	M	611	747	188.7

*Measurements for No. 2 were taken post mortem on 13.05.82.

Table 2. Sizes of neonate *Calloselasma rhodostoma* subjects used in the study. Measurements taken 8.10.82.

Subject	Sex	SVL (mm)	Total (mm)	Weight (g)
1001	F	178 (251)*	199 (275)	7.3 (14.0)
1002	F	177 (239)	198 (262)	6.2 (14.5)
1003	F	180	202	7.5
1004	M	174	197	6.4
1005	M	164	193	5.0
1006	M	169	198	6.7
1007	M	169 (232)	199 (271)	6.0 (13.9)
1008	M	167	196	6.3
1009	F	170	191	5.7
1010	M	174 (213)	194 (241)	6.2 (13.2)
1011	M	170	199	5.2
1012	M	174	196	6.6
1013	M	178	209	7.3
1014	M	182	216	6.9
1015	F	172	194	6.3
1016	M	181 (260)	204 (290)	5.5 (16.8)
1017	M	167	196	5.5
1018	F	163	183	5.9
1019	F	176	198	6.4
1020	M	168	198	6.4
1021	M	177 (224)	198 (252)	6.3 (14.0)
1022	M	157	186	4.5

*Parenthetical values are measurements taken 18.08.83 for those subjects still alive.

time before its next shedding decreased. A more accurate method of identification involved using the pattern of dark opposing triangles which ran along the snakes' ventral side. A coding system was devised whereby one counted the triangles on the right ventral side starting at the neck and recording the number of those triangles which were paired with an opposing triangle on the left ventral side (Fig. 1).

II. HOUSING

In February 1982, the six adult snakes were placed together in a 90 × 60 × 60 cm wooden enclosure fitted with a lockable glass top and front side for observations. The inside of the enclosure simulated the natural environment by including a cypress mulch substrate, three large rocks arranged in crevices, a bowl "pool" for water, and plastic foliage. A wooden "tree" was provided in one corner of the enclosure onto which the snakes might crawl. One or two individuals could be found at any one time coiled under either of the three rock crevices. The cypress mulch provided a suitable substrate in which the snakes blended well due to their cryptically colored patterns. The mulch also formed a suitable substrate for nesting.

When it became necessary to isolate any of the individual snakes, they were housed in separate 60 × 30 × 30 cm cages. Both the floor and two smaller sides of the cages were made of wood; the front and back sides were plexiglass. A lockable wood-framed screen top was used to secure the cage. The cages were divided into a 50 × 30 × 30 cm and a 10 × 30 × 30 cm section by an opaque plexiglass partition. The snakes

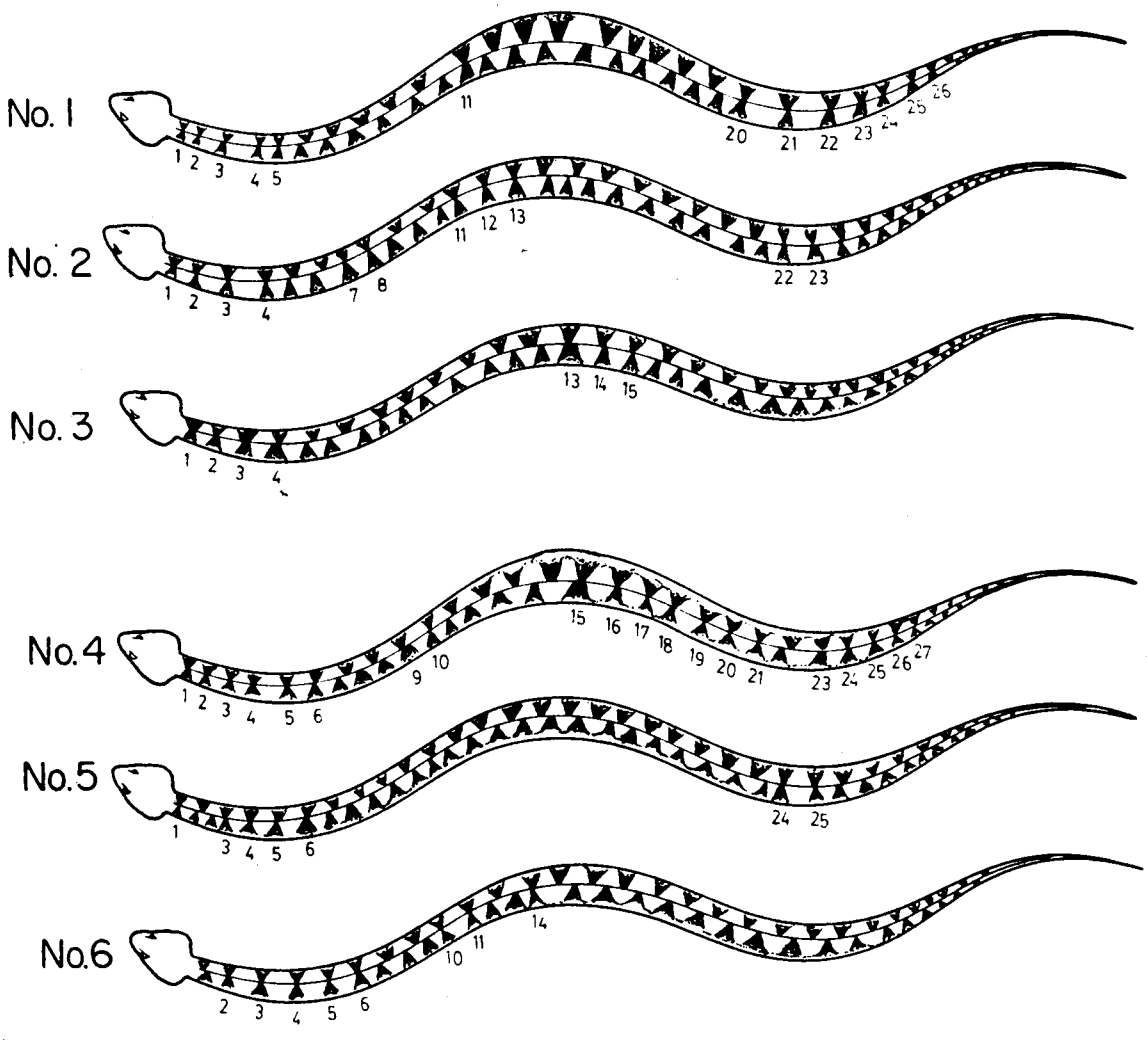


Fig. 1. Method of identifying subject *Calloselasma rhodostoma* by means of dorsal pattern. Small numbers under each diagram represent the code for the connected triangles starting from the neck on the right.

were housed in the larger section that was provided with the same cypress mulch substrate used in the large enclosure. The cages also contained bowls with water as well as wooden shelters under which the snakes could hide.

III. MAINTENANCE

In March 1983, an 11 liter table-top humidifier was used to better maintain a high relative humidity level around the enclosures. Periodic watering of the mulch substrate as well as misting the inside of the cages and enclosure aided in keeping the relative humidity level between 70 and 100%. As completely dry mulch acts as a desiccant promoting dehydration, the periodic watering of the substrate helped in preventing dysecdysis, a condition to which captive Malayan pit vipers are prone.

The temperature in the enclosure varied between 23° and 29°C through a 24 hr cycle. This was accomplished by using a 250-watt infrared heat reflector situated 1 m above and at a 45° angle to the enclosure that remained on for four hours each day during the 12 hr light cycle.

The isolated adult snakes were offered one 20-30 g live laboratory mouse (*Mus musculus*) each week, except for the large female (No. 1) who was offered two mice. If the mouse was not struck within a 10 minute period, it was removed from the cage, killed by a sharp cephalic blow and returned to the cage. If the dead mouse had not been eaten within a 24 hr period it was discarded. When feeding several snakes in the single large enclosure, only freshly killed mice were used.

A multivitamin supplement was added to the fur of the mouse once every two months and if an individual had been feeding irregularly. I used one drop of concentrated Avitron for this purpose. The neonate snakes started feeding on small anoles (*Anolis Carolinensis*) four weeks after hatching and were offered food once every one or two weeks.

As mentioned above, Malayan pit vipers are prone to dysecdysis. When this occurred, the individual was placed in a large plastic container filled with 4 to 6 cm of water and several cloth bags. Normally, soaking the snake in this manner was enough to loosen and remove the old skin; still, one had to be sure that the snake did not have retained eye-caps.

IV. METHODS OF OBSERVATION

Records were kept daily on printed observation sheets (Appendix A). These sheets provided space for records on food, shedding and any unusual events that might be observed. The diagram of the enclosure included on these sheets was used in recording the positions and movements of the animals. The enclosure diagram was also found to be a useful means of keeping track of both the position and weight of the food placed in the enclosure.

As the snakes were kept on a 12/12 reversed light-dark cycle, the majority of the observations were made during the dark phase. Three 25-watt red-ceramic coated light bulbs used during the dark cycle provided acceptable illumination so that observations inside the darkly lit room could be easily made after the observer's eyes became adapted.

More satisfactory observations, however, were conducted using a television monitor in an adjacent room. Two Sony AVC 3250 black and white video cameras equipped with low-light level switches were used and provided bright, clear pictures during the dark cycle. One of the video cameras was attached to a Vicon Pan-Tilt unit so that both the camera direction and angle were controlled remotely. Attached to this camera was a lens in which the focal length, focus, and iris could also be controlled remotely. The other camera was placed in a stationary position either in front of the enclosure or hung from the ceiling directly above the enclosure. When recording on video tape, a Sony Special-Effects Generator was used to produce a split-screen, simultaneous recording from both cameras as well as for producing a smooth picture transition when switching from one camera to the other. A time-date generator recorded continuous time during videorecording. This allowed subsequent analysis of the recorded material to an accuracy of 0.1 sec.

When recording activities with a high level of movement (e.g., male-combat), black and white prints were made with a 35 mm camera connected to an electronic strobe. The black and white prints were invaluable during the subsequent analysis of the videorecordings. The flash of the strobe, whenever a picture was taken, left a 3-frame blackout on the video tape thus marking the exact moment during a behavior sequence when the picture was taken. Due to the speed at which the animals often moved, the exact identification of the subjects was not possible using the videorecordings alone—but were easily made from the prints.

CHAPTER III

MALE COMBAT

I. INTRODUCTION

Reports of combat among male snakes have been receiving increasing interest among herpetologists. First instances of observed male combat appear almost quarterly in the major herpetological journals.

In 1966, a review of male compat by Bogert and Roth listed 28 species of snakes exhibiting this behavior; this was increased to 46 species in 1978 by Shine, and I have uncovered a total of 56 species of snakes have been found to combat (Appendix B). This increase in reports of combat is in part due to an increased understanding of what is occurring, as there has in the past been some confusion (Shaw, 1951; Bogert and Roth, 1966). Generally, this confusion was brought about by the assumption that the two snakes were male and female involved in courtship (i.e., Davis, 1936). The major distinguishing features between courtship and combat (besides the sexes involved) lies in the intensity and the level of interaction between the two individuals. In courtship the female, if receptive, shows little gross body movement (Carpenter, 1977) with the male being the active one of the two. When combating, both snakes are very active, and the intensity of the movements on the part of both appears to be greater than that of an actively courting or copulating male. Combat as it has been reported in

the various snake families is pictured in Fig. 2 and can be summarized as follows:

Boidae. In *Sanzinia madagascariensis*, an arboreal species in which combat is confined to trees, only the posterior trunk and tail are entwined and the heads often out of sight with respect to one another (Carpenter, Murphy, and Mitchell, 1978). A more complex form of combat adapted to a terrestrial life and resembling that of some species of Colubridae and Elapidae is seen in *Python molurus*. This involves a corkscrew-like entwining of the anterior and posterior body parts, with some head raising (Barker, Murphy, and Smith, 1979). In both species vestigial spurs are used in shifting the position of the coils in order to gain a superior position (*P. molurus*) or to throw the opponent from his perch (*S. madagascariensis*) (Carpenter, Murphy, and Mitchell, 1978; Barker, Murphy, and Smith, 1979).

Colubridae. Typical combat in the colubrids involves much entwining (as in *Python molurus*) in a postrate position on the ground. There appears to be tight coiling (Bogert and Roth, 1966), which is probably derived from prey construction, and little or no head raising (one notable exception being the Aesculapian snakes, *Elaphe longissima*).

Elapidae. The type of combat assumed by the Australian elapids and the Asiatic elapid genus Bungarus differs from the mambas and cobras in that the bodies are tightly entwined with a slight horizontal elevation of the heads. In mambas and cobras the anterior portions of the trunk are intertwined with the snouts tilted upwards or even vertical (Bogert and Roth, 1966). In the green mamba, *Dendroaspis viridus*,

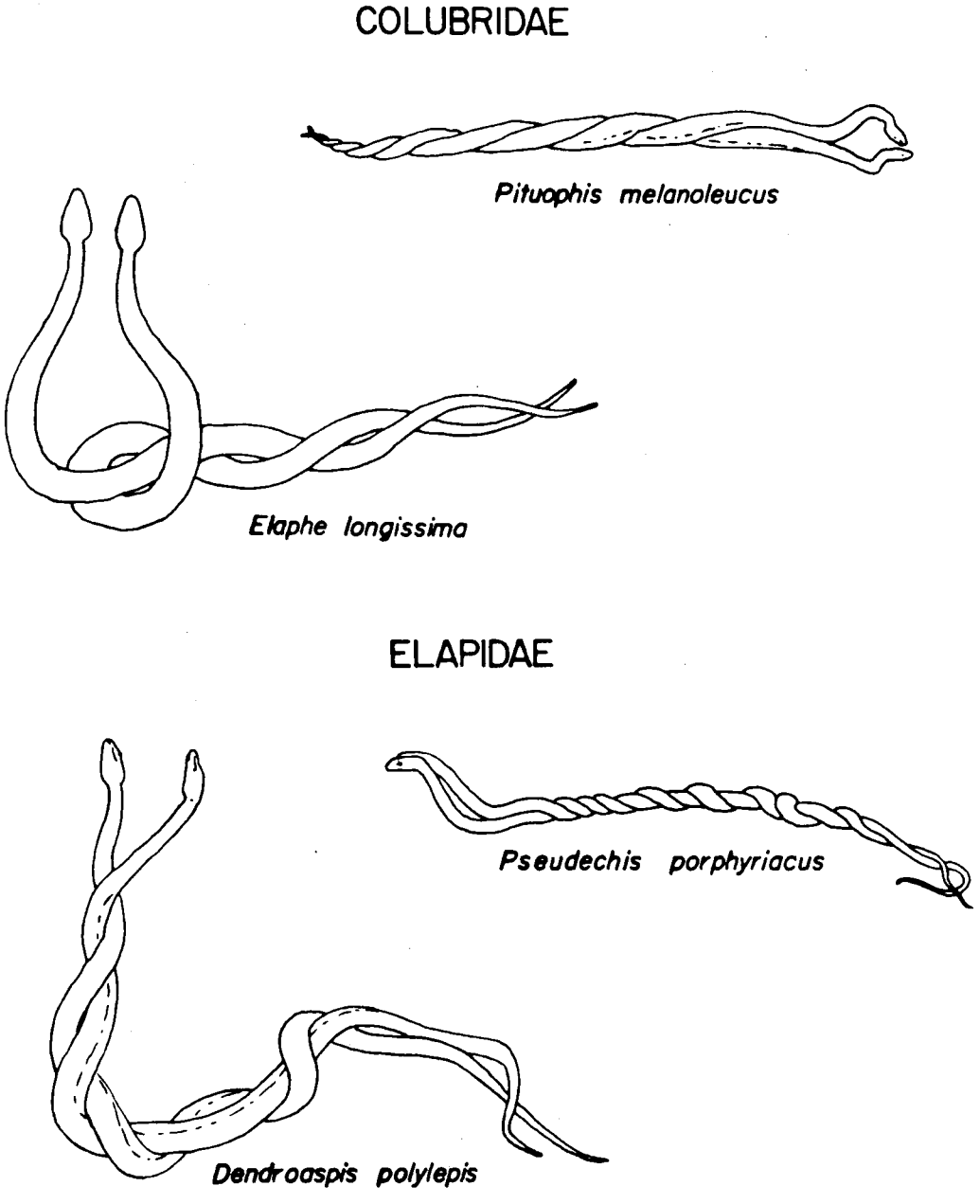
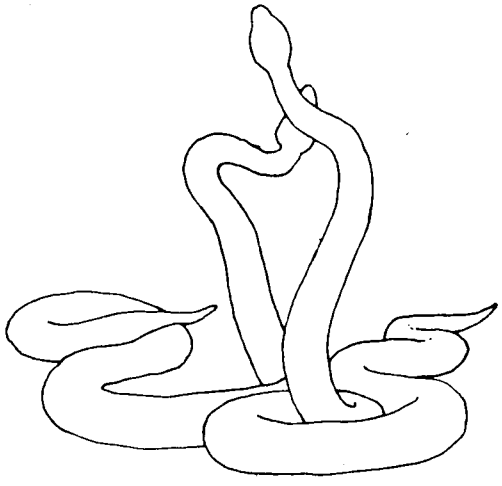


Fig. 2. Positions during combat in various snake families (redrawn from Bogert and Roth, 1966).

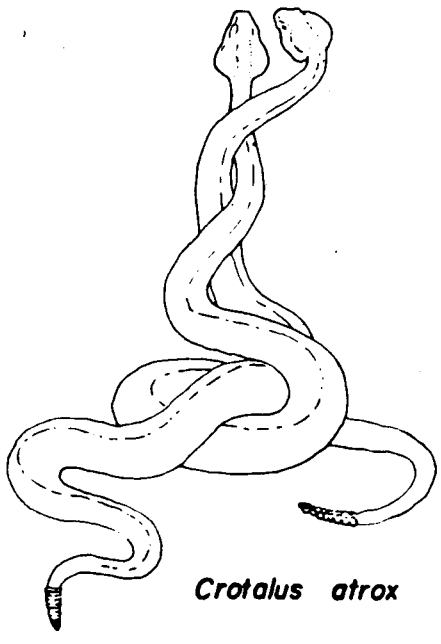
VIPERIDAE

(VIPERINAE)

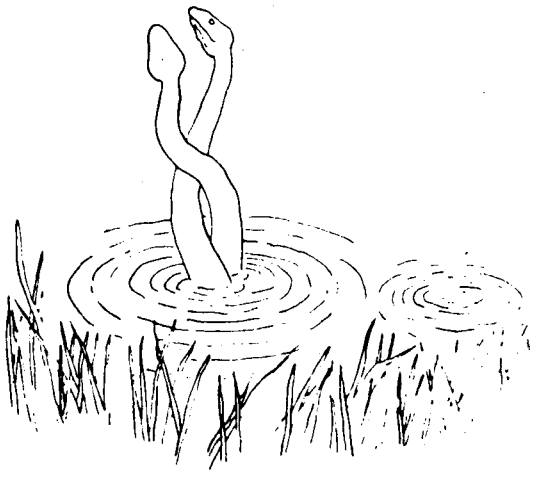


Vipera berus

(CROTALINAE)



Crotalus atrox



Agkistrodon piscivorus

Fig. 2. (continued)

arboreal combat has been observed. The tails were loosely entwined and the anterior portions of the bodies faced away from one another as seen in *Sanzinia madagascariensis* (Dan MacDonald, personal communication).

Viperidae. In general, the viperine and crotaline snakes take on the most spectacular form of combat, whereby a great portion of the anterior trunk is vertically raised and from time to time intertwined. Descriptions of combat in the viperine snake *Vipera berus* share a large number of behaviors found in the descriptions of crotaline combat (see Carpenter and Ferguson, 1977). One reported difference in combat between the two subfamilies is that in the crotalines, the head is oriented in either a horizontal position or pointed downwards during high vertical stances, whereas in viperines the head is more often pointed upwards when the anterior trunk is raised (Bogert and Roth, 1966).

All instances of combat reported on above were observed during daylight. I discovered combat in *Calloselasma rhodostoma* occurring during the scotophase. The following is a description of the first combat I saw in *C. rhodostoma*:

On 17 March 1982 and 7 hours into the dark cycle, the largest female (No. 1) began feeding on one of three dead mice placed in the enclosure. No. 1 was stretched across the enclosure floor while feeding; all three males, who were situated in different corners, extended their necks out from a coiled position towards her and started tongue flicking. Soon afterwards the male (No. 6) lying caudal to the

female proceeded to slide anteriorly up her dorsal side, tongue flicking continually. When No. 6 had advanced approximately two thirds up the female's body, a second male (No. 2), whose head was by this time in very close proximity to the female's dorsal side, tongue flicked the advancing No. 6 and immediately rose to a vertical stance. Immediately No. 6 rose up and combat ensued. At this point the third male (No. 5) withdrew his head to a position low within his coils; the female continued feeding, apparently oblivious to the two males engaged in combat on her back.

During the combat, the two battling snakes would raise more than 30% of their anterior bodies to a nearly vertical position with the angle between the head and neck being from 30 to 45 degrees, a position characteristic of combating crotaline snakes (Carpenter, Gillingham, and Murphy, 1976). From the raised position (Fig. 3), falling was observed often with one or both of the snakes being bashed with such a great force against the wooden or glass side as to cause a very audible "bang." While the snakes were in the raised posture, their posterior bodies and tails were usually in contact with each other, and often these were tightly intertwined. Once, after both snakes fell, this posterior intertwining rapidly progressed to the head in the form of a tight rope, as has been reported for *Pituophis melanolencus* (Shaw, 1951; Bogert and Roth, 1966) and for *Vipera berus* (Andren, 1981).

On several occasions, bouts of tail rattling were observed in one or both of the combating snakes. This occurred while the tail rattling snake was in a stationary upraised position. During tail rattling

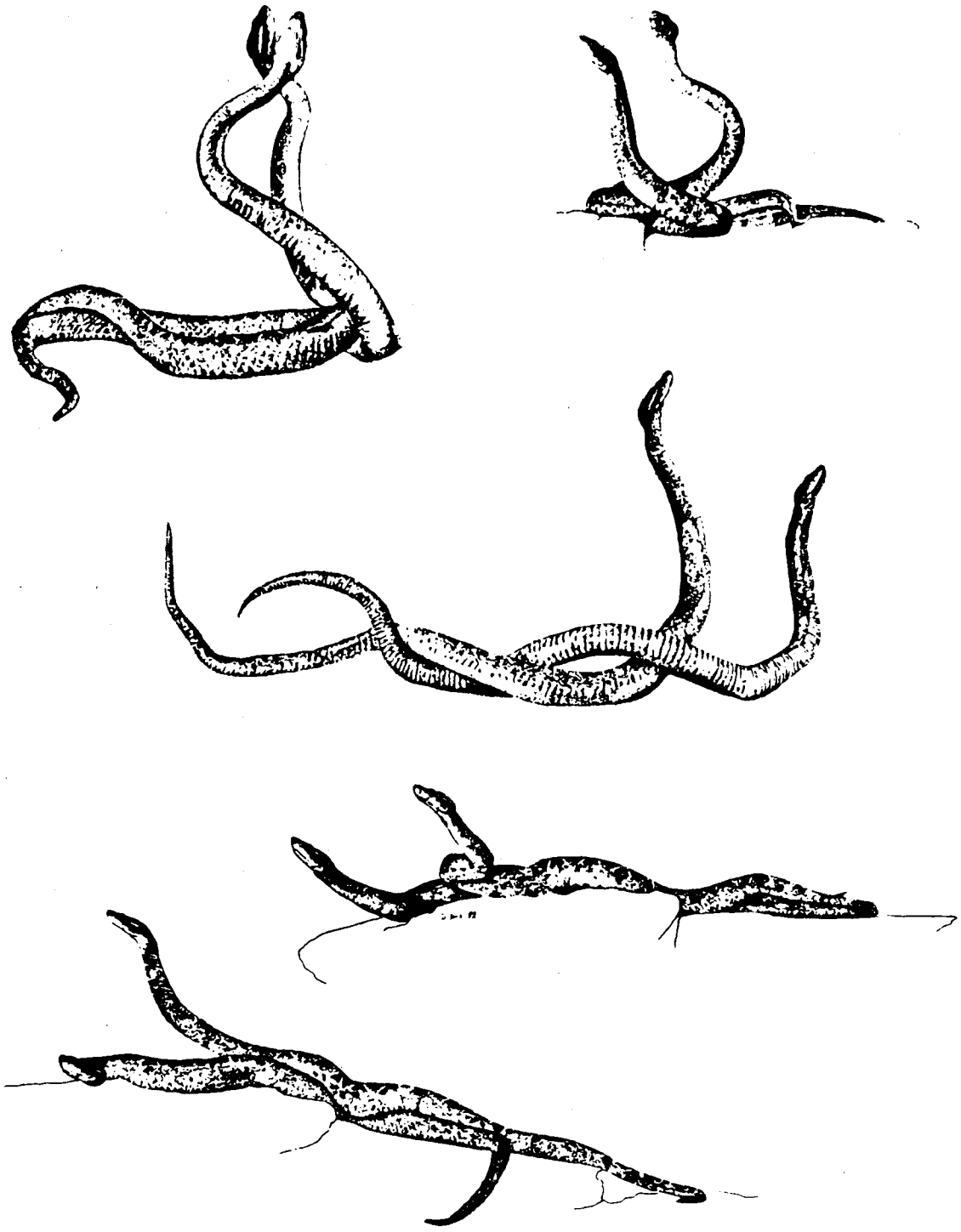


Fig. 3. Positions during combat in *Calloselasma rhodostoma*.

the posterior tip of the tail would rapidly vibrate, emitting a very audible buzzing sound that occurred in pulses lasting approximately one to two seconds. These bouts of tail rattling usually did not last longer than 30 seconds. Frequently both intensive tongue flicking and head vibration were seen occurring together with the pulses of tail rattling.

Burchfield (1982) mentions tail rattling in the cantil (*Agkistrodon bilineatus*) during combat, but otherwise this is not a behavior usually found in descriptions of snake combat. Klauber (1972) specifically states that tail rattling is absent in rattlesnake combat, and Andren (1981) reports tail rattling occurring in both sexes of *Vipera berus* during courtship, but not in combating males.

Over the following three weeks a total of twelve combat sequences were observed, ten of which were recorded on videotape for analysis. The combat sequences, including occasional rests between bouts, ranged in length from 10 min. to a little over an hour (Table 3). Combat was seen only during the dark cycle (a time-lapse surveillance video recorder was used to check for any light cycle activity).

II. DATA COLLECTION

Out of ten videorecorded combat sequences, two complete sequences were determined to be of high enough quality to allow for frame-by-frame analysis. The two combined combat sequences resulted in a total of 84 min. and 54 sec. of combat.

Table 3. Summary of videorecorded combat sequences in *Calloselasma rhodostoma*.

Date	Individuals Involved	Length of Combat
17.04.82	5,6	17 min., 36 sec.
17.04.82	2,6	14 min., 41 sec.
19.04.82*	2,6	36 min., 22 sec.
19.04.82	2,6	1 min., 10 sec.
20.04.82*	2,6	45 min., 30 sec.
20.04.82	2,6	24 min., 57 sec.
20.04.82	5,6	11 min., 59 sec.
20.04.82	2,6	13 min., 30 sec.
26.04.82	2,5	10 min., 50 sec.
26.04.82	2,5	64 min., 25 sec.

*Sequence used in analysis.

After reviewing all of the taped combat sequences, I was able to determine 15 behavioral acts which could be reliably analyzed from the videorecordings.

Direction of Movement

The direction in which one snake was moving with respect to the other was divided into three qualitatively exclusive categories. These categories represent all possible linear movements which affect the general orientation of one snake to the other.

APPROACH. Any lateral movement in one snake which results in decreasing the distance between the moving snake's head or body and the head or body of another snake. This category is restricted to lateral movements in order to avoid any ambiguities associated with vertical raising which has the effect of increasing the (vertical) distance between the moving snake's head and the other's body.

RETREAT. Any lateral movement in one snake which results in increasing the distance between the moving snake's head or body and the head or body of another snake. Again this category is restricted to lateral movements only for the above mentioned reasons.

STABLE. The absence of any lateral movement which has the effect of either increasing or decreasing the distance between the two combating snakes. Movements possible in this category include any upward or downward vertical movements of the anterior body as well as simultaneous lateral movement between the two snakes as occurred while rolling over during tight horizontal entwining (see TWIST below).

Head Height

Three quantitatively different head heights were scored. Although the three categories differed in the amount of variation possible within each, it was determined that any further division would seriously affect the reliability of scoring.

LOW. In this position both the head and the neck ("neck" is defined here as the segment from the point of juncture between the head and trunk and one head length caudal to that point) are on the substrate. The head might be horizontal to the substrate or pointed upwards towards vertical.

MEDIUM. The head is completely raised above the substrate either horizontal to the substrate or pointed towards the vertical. No more than one head length caudal to the point of juncture between the head and trunk (i.e., the neck length) may be raised from the substrate.

HIGH. Both the head and neck (see above) are raised completely off the substrate in this position. This category allows for the greatest variation in the amount of body that is actually raised off the substrate as anywhere from 10 to 50% of the anterior body might be raised off the substrate. It would also be noted that it is not necessary for the head to actually be very high off the ground to be included in this category, as only around 10% of the body need actually be raised, and this can occur at a low body-substrate angle. Still, the anterior segment of the body was usually raised well above the substrate when in this position.

Body Contact

The amount of body contact was divided into five quantitatively exclusive categories. The categories represent all possible levels of contact.

ANTERIOR. This was recorded when any amount of the anterior third of the body came into contact with any part of the opponent snake's body. This category was also recorded when both the upper (anterior) and central thirds of the body made contact with the opponent snake's body.

CENTRAL. Here any part of the central third of the body was in contact with the opponent snake's body. This category could not be scored for if any amount of the anterior or posterior thirds of the snake's body came in contact with the opponent snake.

POSTERIOR. In this category any amount of the posterior third of the body was in contact with any part of the opponent snake's body. Included in this category was any contact between the posterior third and the central third of the snake's body with the opponent snake.

TOTAL. This category was scored when any amount of contact was made between the combined anterior, central, and posterior thirds of the snake's body with that of the opponent snake.

NO CONTACT. The complete absence of any physical contact between the two snakes was required for this category.

Strategic Moves

Four categories of apparent strategical moves were determined. These categories were not necessarily exclusive among themselves, nor were they treated as such in the statistical analysis.

FALL. This was any rapid downward movement of the anterior portion of the snake's body from a high vertical stance not caused by any physical force from the opponent snake. This category is the same as "Tumbling down" in Andren (1981), and appears to be tactical by affording the snake a means by which it might gain a higher vertical position.

TWIST. This category was similar to "Horizontal twisting" as used by Andren (1981) except it was not necessary for the snakes to be in a low horizontal position. This is any tight entwining between any parts of the two snakes—although it usually leads to a tight rope-like entwining in the horizontal position.

TOPPLE. This was identical to "Topping" as described by Carpenter, Gillingham, and Murphy (1976) for the rock rattlesnake (*Crotalus lepidus*), and is any contact between the upper anterior portions of the body while the snakes are in a high stance. The contact could be in the form of pushing, twisting, or entwining.

TUMBLE. This was also identical to "Tumble" as described for *Crotalus lepidus* (Carpenter, Gillingham, and Murphy, 1976), which is a very rapid downward movement caused by the opponent snake, usually occurring during or after TOPPLE. This is also very similar to "Falling apart" as described by Andren (1981).

III. METHODS

The videotaped combat sequences were played back on a variable speed videorecorder with single frame advance and reverse capability. Data were scored on data collection sheets that had columns for each of the categories, a column for the number of the snake being scored, as well as space to record the time which was produced by the time-date-generator. Any time when there was a change in one or more of the categories, the time, snake number and each category was scored as either occurring (a score of 1) or not occurring (a score of 0). This meant each time a category began occurring (e.g., APPROACH) and stopped occurring, it would be recorded, and all other categories would likewise be scored—even if there had not been a change in their status (see Appendix C for sample data sheet). These data were then transcribed onto a computer data file.

A computer program was utilized that converted the collected data on the two combined combat sequences into a total of 4914 sec. intervals (Appendix D). Originally the data were collected to an accuracy of 0.1 sec. Conversion of 84 min. 54 sec. of data taken at this accuracy would have resulted in 49,140 tenth-sec. intervals—an amount deemed unnecessary and too expensive to run. As a result, the data set was reformed by hand to an accuracy of 1 sec. Whenever possible, the information within a 0.1 sec. interval was rounded either up or down to the nearest sec. in order to retain as much information as possible. When deletions were imperative, they were

made at the earlier 0.1 sec. intervals as opposed to the later 0.1 sec. to insure proper transitions between the sec. intervals. This alteration resulted in the deletion of 52 0.1 sec. behavioral transition intervals, representing 13% of the total recorded transitions but less than 1% of the information contained in the combined 1 sec. intervals.

IV. RESULTS

The data were anlyzed for associations among the various categories of behavior scored. This included both intra-individual (Tables 4-6) as well as inter-individual (Tables 7-9) associations. Each cell in Tables 4-9 was tested separately using a G-test (Sokal and Rohlf, 1969) of independence (Fig. 4). As a large number of individual statistical tests were run, only those cells with $p < 0.001$ were considered to be statistically significant. Cells with an expected frequency less than 5.0 were not considered reliable and therefore discarded.

Generally, observed frequencies significantly greater than expected were felt to be "directive," while those observed frequencies significantly less than expected were felt to be "inhibitive." Similar methods of classifying associations can be found in Dingle (1969) and Gillingham (1980). Still, the interpretation of significant associations remains subjective as these associations might imply causation or they might be associated by exclusion (Slater, 1973). An example of such an associated exclusion can be found in Table 7 where NO CONTACT in No. 2 has a very high positive association with NO CONTACT in No. 6.

Table 4. Intra-individual associations with APPROACH seen during combat in *Calloselasma rhodostoma*.

	Snake 2	Snake 6
Low	244 (400.9) ***	211 (647.3) ***
Med	363 (501.6) ***	778 (563.6) ***
High	574 (278.5) ***	517 (295.1) ***
Anterior	5 (2.4)	73 (35.2)
Central	349 (341.3)	385 (436.7) **
Posterior	559 (424.7) ***	392 (302.2) ***
Total	2 (10.6) **	26 (219.4) ***
No Contact	264 (401.6) ***	630 (512.4) ***
Fall	6 (4.1)	79 (31.3) ***
Twist	0 (12.5) ***	3 (18.7) ***
Topple	8 (3.4)	3 (1.8)
Tumble	0 (1.4)	0 (2.5)

Parenthetical numbers represent the expected values. Total number of intervals (= 1 sec.), 4914.

**Indicates $p < 0.01$.

***Indicates $p < 0.001$.

Table 5. Intra-individual associations with RETREAT seen during combat in *Calloselasma rhodostoma*.

	Snake 2	Snake 6
Low	402 (407.7)	1125 (840.2) ***
Med	451 (510.1) ***	659 (731.6) ***
High	348 (283.3) ***	171 (383.1) ***
Anterior	1 (2.4)	0 (45.8) ***
Central	202 (347.1) ***	457 (566.9) ***
Posterior	454 (431.9)	275 (392.3) ***
Total	0 (10.8) ***	536 (284.9) ***
No Contact	544 (408.4) ***	687 (665.2)
Fall	2 (4.2)	0 (40.6) ***
Twist	1 (12.7) ***	0 (24.3) ***
Topple	0 (3.4)	0 (2.4)
Tumble	0 (1.5)	0 (3.2)

Parenthetical numbers represent the expected values. Total number of intervals (= 1 sec.), 4914.

**Indicates $p < 0.01$.

***Indicates $p < 0.001$.

Table 6. Intra-individual associations with STABLE seen during combat in *Calloselasma rhodostoma*.

	Snake 2	Snake 6
Low	1022 (859.5) ***	776 (624.5) ***
Med	1273 (1075.4) ***	402 (543.8) ***
High	237 (597.2) ***	275 (284.7)
Anterior	4 (5.2)	42 (34.0)
Central	869 (731.7) ***	583 (421.4) ***
Posterior	754 (910.5) ***	319 (291.5)
Total	42 (22.7) ***	154 (211.7) ***
No Contact	863 (861.0)	355 (494.4) ***
Fall	9 (8.8)	23 (30.2)
Twist	51 (26.8) ***	58 (18.0) ***
Topple	6 (7.2)	3 (1.8)
Tumble	6 (3.1)	8 (2.4)

Parenthetical numbers represent the expected values. Total number of intervals (= 1 sec.), 4914.

**Indicates $p < 0.01$.

***Indicates $p < 0.001$.

Table 7. Inter-individual associations of all scored behaviors seen occurring between No. 2 and No. 6 (*Calloselasma rhodostoma*) during combat.

	Approach 6	Retreat 6	Stable 6	Low 6	Med 6	High 6	Anterior 6	Central 6	Posterior 6	Total 6	No Contact 6	Fall 6	Twist 6	Topple 6	Tumble 6
Approach 2	365 (361.9)	654 (469.9) ***	162 (349.2) ***	364 (507.6) ***	447 (442.0)	370 (231.4) ***	3 (27.6) ***	616 (342.5) ***	296 (237.0) ***	1 (172.1) ***	265 (401.8) ***	25 (24.5)	0 (14.7) ***	2 (1.4)	2 (1.9)
Retreat 2	563 (368.0) ***	541 (477.8) ***	97 (355.1) ***	459 (516.2) ***	431 (449.5)	311 (235.4) ***	16 (28.1) **	174 (348.3) ***	176 (241.0) ***	288 (175.0) ***	544 (408.6) ***	72 (24.9) ***	1 (14.9) **	0 (1.5)	0 (2.0)
Stable 2	578 (776.0) ***	760 (1007.3) ***	1194 (749.2) ***	1289 (1088.2) ***	961 (947.6)	282 (496.2) ***	96 (59.2) ***	633 (734.2) ***	513 (508.0)	427 (368.9) ***	863 (861.5)	5 (52.6) ***	60 (31.4) ***	4 (3.1)	6 (4.1)
Low 2	231 (511.2) ***	796 (663.6) ***	641 (493.2) ***	7331 (716.9) ***	270 (624.2) ***	67 (326.9) ***	104 (39.0) ***	457 (483.7)	133 (334.7) ***	320 (243.0) ***	654 (567.5) ***	0 (34.6) ***	46 (20.7) ***	1 (2.0)	4 (2.7)
Med 2	910 (639.6) ***	525 (830.3) ***	652 (617.1)	714 (897.0) ***	955 (781.0) ***	418 (409.0)	5 (48.8) ***	507 (605.2) ***	388 (418.8)	388 (304.1) ***	799 (710.1) ***	77 (43.3) ***	5 (25.9)	0 (2.5)	1 (3.4)
High 2	365 (355.2)	634 (461.1) ***	160 (342.7) ***	67 (498.1) ***	614 (433.7) ***	478 (227.1) ***	6 (27.1) ***	461 (336.0) ***	465 (233.0) ***	8 (168.9) ***	219 (394.4) ***	25 (24.1)	10 (14.4)	5 (1.4)	3 (1.9)
Anterior 2	2 (3.1)	1 (4.1)	7 (3.0)	4 (4.3)	0 (3.7)	6 (2.0)	5 (0.2)	4 (2.9)	1 (2.0)	0 (1.5)	0 (3.4)	0 (0.2)	2 (0.1)	0 (0.0)	4 (0.0)
Central 2	311 (435.2) ***	334 (564.9) ***	748 (420.0) ***	545 (610.3) ***	475 (531.4) ***	400 (278.3) ***	53 (33.2) ***	1079 (411.8) ***	287 (284.9)	0 (206.9) ***	0 (483.2) ***	97 (29.5) ***	4 (17.6) ***	0 (1.7)	1 (2.3)
Posterior 2	534 (541.5)	931 (703.0) ***	302 (502.5) ***	972 (759.4) ***	520 (661.3) ***	275 (346.3) ***	24 (41.4) ***	340 (512.4) ***	695 (354.6) ***	708 (257.5) ***	0 (601.2) ***	4 (36.7) ***	16 (21.9)	2 (2.2)	3 (2.9)
Total 2	2 (13.5) ***	0 (17.5) ***	42 (13.0) ***	37 (18.9) ***	2 (16.5) ***	5 (8.6)	33 (1.0)	0 (12.8) ***	3 (8.8)	9 (6.4)	0 (15.0) ***	0 (0.9)	39 (0.5)	3 (0.1)	0 (0.1)
No Contact 2	630 (512.1) ***	687 (664.8)	354 (494.1) ***	552 (718.2) ***	842 (625.3) ***	277 (327.5) ***	0 (39.1) ***	0 (484.6) ***	0 (335.3) ***	0 (243.5) ***	1671 (568.6) ***	1 (34.7) ***	0 (20.7) ***	1 (2.0)	0 (2.7)
Fall 2	4 (5.2)	4 (6.8)	9 (5.0)	4 (7.3)	3 (6.4)	10 (3.3)	0 (0.4)	12 (4.9)	5 (3.4)	0 (2.5)	0 (5.8) ***	2 (0.4)	0 (0.2)	0 (0.0)	1 (0.0)
Twist 2	0 (15.9) ***	0 (20.7) ***	52 (15.4) ***	41 (22.3) ***	0 (19.5) ***	11 (10.2)	37 (1.2)	0 (15.1) **	8 (10.4)	7 (7.6)	0 (17.7) ***	0 (1.1)	49 (.06)	2 (0.1)	1 (0.1)
Topple 2	6 (4.3)	0 (5.6)	8 (4.1)	2 (6.0)	1 (5.2)	11 (2.7)	3 (0.3)	4 (4.1)	5 (2.8)	1 (2.0)	1 (4.8)	0 (0.3)	2 (0.2)	0 (0.0)	2 (0.0)
Tumble 2	0 (1.8)	0 (2.4)	6 (1.8)	3 (2.6)	0 (2.2)	3 (1.2)	3 (0.1)	1 (1.7)	1 (.12)	1 (0.9)	0 (2.0)	0 (0.1)	3 (0.1)	0 (0.0)	1 (0.0)

Parenthetical numbers represent the expected values. Total number of intervals (= 1 sec.), 4914.

**Indicates $p < 0.01$.

***Indicates $p < 0.001$.

Table 8. Associations between preceding acts in No. 2 and acts occurring one interval (= 1 sec.) later in No. 6 (*Calloselasma rhodostoma*).

Acts Preceding—Snake 2		Acts Following—Snake 6: APPROACH Low	APPROACH Med	APPROACH High	RETREAT Low	RETREAT Med	RETREAT High	STABLE Low	STABLE Med	STABLE High
APPROACH	Low	187 (9.9) ***	12 (36.6) ***	2 (24.3) ***	23 (52.9) ***	1 (31.0) ***	0 (8.0) **	0 (36.5) ***	4 (18.9) ***	2 (12.9) **
	Med	2 (28.4) ***	290 (104.7) ***	22 (69.6) ***	181 (151.4)	56 (88.7) ***	49 (23.0) ***	53 (104.4) ***	4 (54.0) ***	4 (37.0) ***
	High	0 (23.5) ***	154 (86.6) ***	117 (57.6) ***	41 (125.3) ***	52 (73.4)	80 (19.0) ***	4 (86.4) ***	81 (44.6) ***	18 (30.6)
RETREAT	Low	4 (25.2) ***	0 (93.0) ***	0 (61.8) ***	583 (134.4) ***	0 (78.7) ***	0 (20.4) ***	0 (92.7) ***	0 (47.9) ***	0 (32.9) ***
	Med	0 (11.1) ***	6 (41.0) ***	91 (27.3) ***	23 (59.3) ***	134 (34.7) ***	0 (9.0) **	2 (40.9) ***	0 (21.9) ***	3 (14.5) **
	High	0 (7.3) **	7 (27.1) ***	10 (18.0)	8 (39.2) ***	69 (22.9) ***	36 (6.0) ***	0 (27.0) ***	33 (14.0) ***	8 (9.6)
STABLE	Low	3 (33.9) ***	18 (125.1) ***	13 (83.1) ***	158 (180.9)	53 (106.0) ***	0 (27.5) ***	531 (124.8) ***	1 (64.5) ***	13 (44.2) ***
	Med	14 (36.9) ***	250 (136.2) ***	138 (90.5) ***	108 (196.9) ***	119 (115.4)	0 (29.9) ***	18 (135.8) ***	163 (70.2) ***	50 (48.1)
	High	1 (34.7) ***	41 (127.8) ***	124 (84.9) ***	0 (184.8) ***	175 (108.2) ***	6 (28 1). ***	168 (127.5) ***	115 (65.9) ***	177 (45.2) ***

Parenthetical numbers represent the expected values. Total number of intervals, 4914.

**Indicates $p < 0.01$.

***Indicates $p < 0.001$.

Table 9. Associations between preceding acts in No. 6 and acts occurring one interval (= 1 sec.) later in No. 2 (*Calloselasma rhodostoma*) during combat.

Acts Preceding—Snake 6		Acts Following—Snake 2								
		APPROACH			RETREAT			STABLE		
		Low	Med	High	Low	Med	High	Low	Med	High
APPROACH	Low	79 (28.3) ***	112 (42.1) ***	8 (66.6) ***	63 (46.7)	56 (52.3)	4 (40.4) ***	232 (117.2) ***	8 (147.8) ***	7 (27.5) ***
	Med	0 (10.5) **	147 (15.6) ***	27 (24.6)	0 (17.2) ***	0 (19.3) ***	0 (14.9) ***	29 (43.3)	2 (54.5) ***	5 (10.2)
	High	61 (46.2)	10 (68.8) ***	399 (108.8) ***	36 (76.2) ***	36 (85.5) ***	135 (66.0) ***	8 (191.4) ***	230 (241.3)	14 (44.9) ***
RETREAT	Low	0 (0.7)	0 (1.0)	1 (1.6)	12 (1.1)	0 (1.3)	0 (1.0)	0 (2.9)	1 (3.6)	0 (0.7)
	Med	102 (41.8) ***	35 (62.2) ***	67 (98.4) **	0 (68.9) ***	258 (77.3) ***	50 (59.6)	13 (173.1) ***	263 (218.1) **	52 (40.6)
	High	0 (9.9)	6 (14.7) ***	4 (23.3)	0 (16.3) ***	7 (18.3) **	157 (14.1) ***	20 (41.0) ***	0 (51.7) ***	5 (9.6)
STABLE	Low	0 (11.8)	11 (17.6) ***	7 (27.8)	3 (19.4) ***	1 (21.8) ***	1 (16.8) ***	119 (48.8) ***	3 (61.5) ***	12 (11.5) ***
	Med	1 (75.2) ***	4 (111.9) ***	19 (176.9) ***	288 (123.9) ***	0 (139.0) ***	1 (107.3) ***	504 (311.3) ***	685 (392.4) ***	9 (73.1) ***
	High	1 (19.6)	38 (29.1) ***	42 (46.0)	0 (32.2)	93 (36.2) ***	0 (27.9) ***	5 (81.0) ***	81 (102.1) ***	133 (19.0) ***

Parenthetical numbers represent the expected values. Total number of intervals, 4914.

**Indicates $p < 0.01$.

***Indicates $p < 0.001$.

APPROACH 2/RETREAT 6
Association

	Intervals with RETREAT 6	Intervals without RETREAT 6	
Intervals with APPROACH 2	654 (469.9)	527	1181
Intervals without APPROACH 2	1301	2432	3733
	1955	2959	N 4914

$G = 2(654 \ln 654 + 527 \ln 527 + 1301 \ln 1301 + 2432 \ln 2432 + 4914 \ln 4914 - 1181 \ln 1181 - 3733 \ln 3733 - 2959 \ln 2959 - 1955 \ln 1955)$

$= 155.2$ (Distributed as χ^2 with 1 df)

Fig. 4. Statistical analysis used in determining the degree of association between two behaviors. Parenthetical value is the expected interval frequency assuning no effect between behaviors.

In both No. 2 and No. 6 APPROACH was positively associated ($p < 0.001$) with a HIGH head position. In No. 6 there was likewise a positive association between APPROACH and a MEDIUM head position (Table 4). This association would indicate some signal function as in both snakes a preceding combination of APPROACH-HIGH was positively associated with a following APPROACH-HIGH response on the opposing snake (Tables 6-7). Also in both snakes APPROACH is positively associated with RETREAT in the opposing snake (Table 5). This was generally seen as one snake simply following the other and could not be considered as chasing (Gillingham, 1980) as no vigorous retreating movements were observed.

RETREAT in No. 2 was positively associated with a HIGH head position while in No. 6 it was positively associated with a LOW head position (Table 5). In No. 2 RETREAT-HIGH was positively associated with a RETREAT-MEDIUM, RETREAT-HIGH, as well as a STABLE-MEDIUM response in No. 6 (Table 8). RETREAT-LOW in No. 6 was most often followed by a RETREAT-LOW in No. 2, but a low expected frequency did not allow for any statistical testing (Table 9). In both snakes RETREAT was positively associated with RETREAT in the opposing snake (Table 7).

STABLE was positively associated with LOW in both No. 2 and No. 6 as well as MEDIUM in No. 2 (Table 6). In both snakes STABLE-LOW was positively associated with STABLE-LOW in the opposing snake (Tables 8-9). In this sense a STABLE-LOW combination appears to be the least threatening position as it does not provoke either an APPROACH or

RETREAT response in the opposing snake. From Table 7, p. 30, it can be s en that LOW is positively associated in both snakes with LOW in the other as well as having a negative association with both MEDIUM and HIGH. In No. 2 there exist positive associations between LOW and RETREAT and STABLE, while a LOW in No. 6 is negatively associated with RETREAT. In both snakes there is a negative association between LOW and APPROACH in the opposing snake. Further evidence for the importance of the head position in antagonistic encounters can be seen in the negative association effect that HIGH has on STABLE in both snakes. I feel that there is good evidence that HIGH in both snakes is having a "directive" effect on HIGH in the opposing snake and an "inhibitive" effect on LOW in the opposing snake. Although APPROACH was negatively associated with LOW in both snakes, it was found to have a positive association with HIGH in snake No. 6 only.

V. DISCUSSION

The question "Why do males combat?" is a topic still open to debate. Possible interpretations that have been considered include: sex discrimination, homosexual behavior, social dominance, territoriality, and defense of an area for the possession of a female. Shaw (1951) determined that sex discrimination was unlikely due to the time involved and the fact that snakes show a high degree of sex discrimination through their chemical sense. Combats between *Pituophis* males have been observed to last over an hour (Shaw, 1951), a length of time in which the snakes are oblivious to any environmental stimuli (Bogert and

Roth, 1966) and thus open to predator attack. Combat in *C. rhodostoma* was observed lasting anywhere from 5 minutes to a little over an hour. While the snakes were not completely oblivious to environmental stimuli during this time, they would nonetheless attract a potential predator's attention. It would be hard to imagine a selective pressure for sex discrimination at such a great risk and energy expenditure, especially when one considers the fact that males can differentiate between females that are and are not in oestrous (Noble, 1937).

For Shaw, a more reasonable interpretation was that combating males were exhibiting a form of homosexual behavior (Shaw, 1951). Noble (1937) noted that movement in *Coluber c. constrictor* appears to stimulate other snakes to greater sexual activity. This led Shaw to believe that once greatly excited by movement, a male might attempt to breed or court another male. Olfactory cues would be overridden by his high level of excitement, and this would cause the "courted" male to respond with defensive combat. In support of this view, Shaw offered several examples in which hemipenial intromission did actually occur in combat. Klauber (1972) held to a similar view in that he believed combat probably resulted from some kind of sexual impulse.

Shaw's interpretation was criticized by Bogert and Roth (1966) who felt he relied too much on captive snakes, as well as the rarity of intromission between combating males in their natural environment. They were more in favor of a territorial defense around a female notion (here called female defense), supported by more naturalistic observations, such as those by Leloup (1964) and Prior (1933).

Leloup observed a group of mambas (*Dendroaspis jamesoni*) in a "semi-free" enclosure closely approximating their natural environment. Here as many as eight males were attracted to a single female during the peak of their sexual activity (it should be noted that the population dynamics of the enclosure did seem to be somewhat less than naturalistic). This brought about combat among the males in which the courting male would "throw himself upon his antagonist" (Leloup, 1964) with the winner of the contest returning to the female to continue courtship.

While observing the common adder (*Vipera berus*) in the field, Prior (1933) noted that a single male was seen to fight off three other males while it was courting a female and returning to the female after each bout. In another study of *Vipera berus* in the field Andren (1981) found that in all instances of combat (35) the "defending" male was either courting or lying in close proximity to a female. It was also noted in the same account that combat and courtship only occurred in recently sloughed individuals.

Despite occasional anthropomorphism in the description of combat by some authors (e.g., Leloup, 1964; Prior, 1933), the female defense view of male combat does seem to be the strongest interpretation. This is due not only to the greater number of combat observations occurring in the presence of a female during the breeding season, but also the frequency with which this has been observed in the field. On several occasions I observed in *C. rhodostoma* one of the combating males to crawl over to and, on one occasion, coil around a female resting nearby.

This usually occurred between combat bouts and did not appear to have an effect on the other male. Again, the "naturalness" of the environment could very easily be questioned as the single enclosure contained 3 males and 3 females.

The social dominance interpretation of combat is supported by Barker, Murphy, and Smith (1979), who reported the formation of a linear social hierarchy among four male Indian pythons (*Python molurus*). The hierarchy corresponded to the number of successful copulations with the single female. However, the authors pointed out that this hierarchy appears to exist only prior to mating, with agonistic behavior between the males ceasing after copulation.

Sexual Size Dimorphism

Assuming the correctness of either the female defense or male hierarchy interpretations, it follows that selection pressure for large males, who would be at an advantage in such contests, would be the individuals to pass their genes on in future generations.

Theories as to the function and evolution of size-differentiation between the sexes exhibited in many animals is only now starting to build momentum in the literature. Taking the initiative from Darwin (1878), many of these theories center upon selection by the sexes (Schoener, 1977; Shine, 1978; Trivers, 1972). Still, there exist many cases where sexual selection appears to be either nonoccurrent or playing only a partial role in the evolution of sexual size-dimorphism (Kolata, 1977; Ralls, 1976; Selander, 1966; Schoener, 1977). With

respect to the Serpentes, this problem has been grossly overlooked. The vast majority of literature concerned with sexual dimorphism in snakes has focused on the means of identifying the sexes. This has resulted in masses of data covering differences in ventral and subcaudal scute counts (Boulenger, 1893; Kopstein, 1941; Pitman, 1974; Pope, 1935; Smith, 1943; Wall, 1921; Wright and Wright, 1957). These have been shown to be a poor indicator of actual size differences between the sexes (Kopstein, 1941). The fact that snakes show relatively indeterminate growth only complicates matters as it has been shown that males of several snake species tend to reach sexual maturity at a younger age (thus smaller size) than females. This would force the means of adult size ranges to be biased in favor of females (Klauber, 1973; Fitch, 1981). Locality differences in size ranges also tend to vary greatly (Klauber, 1972; Kopstein, 1941) which could have an effect on the overall mean size if the proportion of each sex is not controlled for with respect to locality. When comparing differences in sizes between the sexes, the best possible measurements to look at would be upper portions of the size ranges (Klauber, 1972). Unfortunately such data are practically nonexistent in the literature.

Shine (1978) analyzed 250 species of snakes representing the eight snake families in which he could find size data and showed that only 14.7% of those snakes samples have been observed to exhibit male combat. Shine also found in 65.6% of the species in the analysis that the females were larger than the males. When this is compared with only

15% of females being larger in those species with male combat, the extent of the selection pressure for large males in combat species is striking.

In the sexual selection model proposed by Trivers (1973) the sex which contributes less parental investment will compete for the other sex. In a study of *Anolis garmani* (Trivers, 1973), reproductive success was analyzed for both males and females and a positive correlation was found for both sexes with respect to size. But this correlation was found to be stronger for males than females, with males growing at a faster rate and obtaining an adult weight two and one half times greater than that of the female. Here it was assumed that females represented the sex with the greatest parental investment due to their greater energy requirement for reproduction. From this, one would expect that in snake species with male combat there would be greater parental investment on the part of the females than in those species of snakes without combat. Such a difference has not yet been found, probably due to the difficulty in defining parental investment in quantifiable terms.

Ignoring which sex is larger, Selander (1966) states that if ecological competition is reduced between the sexes, sexual dimorphism will be an advantage for those species. Along these same lines Schoener (1977) found, while working with island *Anolis* species, that there was lower dimorphism on islands with higher numbers of congeners than species on less species-rich islands, and that there was lower sexual dimorphism on islands with a large diversity of species than

on smaller islands with fewer species. It was further found that *Anolis* on small colonized satellite islands showed greater sexual dimorphism than on the "home" island and that in species with overlapping ranges there was greater size dimorphism in allopatry than sympatry. Such studies in snakes are generally lacking, though mention of size changes correlated with longitude and latitude can be found (Kopstein, 1941; Wright and Wright, 1957; Klauber, 1972). According to those references in which the respective sizes of the sexes are given, it appears that in *C. rhodostoma* it is the female who is the larger of the sexes (Smith, 1943; Taylor, 1965).

Kelleway and Brain (1982) proposed that in *Vipera berus* (a species with larger females than males) combat can also take place over food. This being the case, the larger female would be predisposed to becoming victorious and thus dominant (sic). This would increase the likelihood that a gravid female would obtain the disputed food item. Again, this was not found to be the case with *C. rhodostoma*.

In the two combat sequences analyzed here, large size did not appear to be a factor in the outcome of combat. Neither time were any vigorous retreating movements observed—both snakes seemed to simply lose interest in one another. In April 1983, three combat bouts were observed, in the same enclosure as before, between No. 5 and No. 6. All three combat bouts ended with vigorous retreating movements by No. 6. Both No. 5 and No. 6 were comparable in size. What exactly determines who will be the victor in combat in *C. rhodostoma* remains to be found.

Why Large Females?

Up to now the majority of work done on sexual dimorphism has been concerned with birds, the general feeling being that the female is most likely the optimal size with respect to the niche and that the male size (normally greater than the female) is influenced by intrasexual selection (Amadon, 1959). In snakes, species in which males are larger than females represent the minority—even in those snakes with intrasexual selection for large males, we find females being larger in 15% of the species (Shine, 1978). Theories as to possible selective pressures for large females are few. Probably the best review of possible selective pressures for large females is presented by Ralls (1976) who looked at five influences on mammalian size which could favor large females: sexual selection acting upon the females of a species rather than the males, female dominance over males, reduction of intersexual competition for food, more intense competition for some resource by females than by males, and various advantages associated with being a "big mother."

Sexual selection could be acting upon the females of a species rather than the male. In mammals with larger females, such as the golden hamsters, seals, and most bats, the males make little or no parental investment. In the New World primates and in mongooses there is a high degree of male parental investment, yet there is no direct correlation between male or female size and the amount of parental investment. In the Weddel seal (*Leptonychotes weddelli*), greater sac-winged bat (*Saccopteryx bilineata*), and noctule (*Nyctalus noctula*; a bat), males possess harlems, and still one finds females

which are larger. The idea that larger females are more aggressive does not always hold (Ralls, 1976). In species where the female is larger and yet the males are more aggressive and show intrasexual selection such as horns, large size may be advantageous in intermale competition for females but does not result in males exceeding female size. This may occur when large size in males has an advantageous effect in some other respect, there is some even larger selective pressure for large size in females, or large size is not important in intermale competition (Shine, 1978; Ralls, 1976). This idea is particularly important when one considers the species of snakes with male combat in which the female is larger (e.g., *C. rhodostoma*, see above).

Female dominance and matriarchy are found in some raptors where the females are larger and dominant over the males, thus preventing them from being preyed upon by the males and allowing them to protect the young from the males. The assumption that this would not be able to occur if the female was smaller than the male is implicit to this prediction. This can also be seen in flying squirrels, where the female is larger and holds a territory. This probably would not be possible if it were not for the female's superior size (Ralls, 1976). The idea of female dominance and matriarchy in snakes has, to my knowledge, never been investigated nor has it been reported. My observations on *C. rhodostoma* have found interactions between the sexes to be limited to interactions relating to courtship and mating.

Again, in the raptors one often sees a differential utilization of the niche. Here the larger size of the female is seen as a means

of reducing the intersexual competition for food. This explanation does not answer the question as to which sex should be larger with all other things being equal. One cannot know whether dimorphism arose to an increased utilization of the niche or if differential utilization arose as a result of size dimorphism brought on by something else (Ralls, 1976). This possibility was investigated by Schoener (1977) in his work on *Anolis* (see above), only here the males were the larger sex. Differential niche utilization could very well be taking place in the serpentes, especially those with large size differences. This would tend to have a stabilizing effect on size dimorphism; but the problem remains—what originally brought on the differentiation of size between the sexes?

There could be a selective pressure for large females due to a more intense competition for some necessary resource such as food. This would be particularly important when the lack of some resource is more critical to female reproductive success than to male reproductive success. Increased competition with males could be another factor influencing the acquisition of territories by large female flying squirrels (see above) (Ralls, 1976). This also connects well with the findings of Downhower (cited in Kolata, 1977) that large females are at an advantage when it is necessary to have bodily reserves accumulated and stored before breeding. This might be a reason for the larger body size in female adders (*Vipera berus*) despite the fact that there is active male competition in the form of combat for reproductive access to females. This idea is further substantiated by the fact that female *V. berus* show a biennial reproductive cycle

in their northern ranges (Steward, 1971). Biennial and triennial reproductive cycles have been shown to be correlated with the time necessary to accumulate fat bodies responsible for yolk formation (Gibbons, 1972) in Canebrake rattlesnakes, so it would seem reasonable that similar demands are influencing the reproductive cycle of *Vipera berus*. I have found *C. rhodostoma* to be an annual breeder or at least so when in captivity with an unlimited food supply. Generally, it has been my finding that the females accepted food more readily and appeared to have a more voracious appetite. This could well be due to their need to acquire greater quantities of food for reproduction. The Malayan pit viper is known to lay as many as 30 eggs per clutch (Smith, 1943)—a number probably large enough to cause the ability to accumulate a large amount of bodily reserves in a short period of time to have a selection value. This would then follow Downhower's findings well.

Ralls (1976) also argued that in mammals, larger females may produce a greater number of offspring and or larger (fitter) offspring. This idea is in opposition with that of Trivers (1972) which states that in mammals and birds with low, fixed clutches, selection for smaller females could be occurring because larger female size may be relatively unimportant in reproductive success of the female. In many fish, lizards, and salamanders, the female reproductive success is measured by clutch size which is correlated strongly within species with size. Vitt, however, reported that in some "sit-and-wait" strategy lizards which depend on crypticity to escape from predators, morphology plays a very important role in clutch size. In the

iguanid lizard *Platynotus semitaeniatus*, which hides in rock crevices, a small, thin body morphology is important to their survival. Here low clutch size helps overall reproductive success by maintaining the proper body morphology (Vitt, 1981). In a comparative study by Fitch (1970), it was found that within species, variation in clutch size with female size is significant. An extreme example of this can be seen in *Python reticulatus*, where small females (10-11½ feet) had clutches of 14, 15, and 16, whereas large females (near a maximum of 26 feet) had clutches of 96 and 103. It should be stressed that such variation occurs only within a species. This point can be made clear in an intergeneric comparison between a small (large) garter snake with a clutch size of greater than 60 and a large (small) python clutch size of 14. An exception to this general rule was shown by Gibbons (1972) in the Canebrake rattlesnake whose mean litter size did not appear to increase as a result of an increase in female body size but was correlated with the fat body weight in the female.

CHAPTER IV

COURTSHIP AND MATING

I. INTRODUCTION

Courtship and mating have been well studied in several snake species (Davis, 1936; Noble, 1937; Gillingham, 1979) of the widespread and cosmopolitan family Colubridae. But as early as 1936, Davis noted the existence of important and unfortunate gaps in our knowledge of serpent courting and mating behavior—especially among the elapid and viperid snakes. Since then there have been detailed descriptive reports on the courtship and mating activities of an elapid (*Ophiophagus hannah*, Oliver, 1956), the viperines *Vipera berus* (Andren, 1981) and *V. xanthina* (Murphy and Barker, 1980), and a crotaline (*Sisturus catenatus tergeminus*, Chiszar, Scudder, Smith, and Radcliffe, 1976). In these reports, reproductive behavior occurred during the day time. The majority of crotaline snakes appear to be nocturnal or at least crepuscular, and it is generally assumed that this has prevented thorough descriptions of crotaline courtship and mating (Davis, 1936; Klauber, 1972). Two notable exceptions are the observations of nocturnal courtship and mating in the crotalines *Agkistrodon contortrix* Fitch, 1960) and *Bothrops schlegeli* (Antonio, 1980).

II. MATERIALS AND METHODS

Courtship and mating in *Calloselasma rhodostoma* were observed and videorecorded on two different occasions as they occurred in a captive environment. All activity was observed during the snakes' dark phase.

On 6 April 1983, the male No. 6 was placed in the 90 × 60 × 60 cm wooden enclosure, which at that time was occupied only by the female No. 4. Female No. 2 was placed in the enclosure with Nos. 4 and 6 on 21 April 1983. Recordings were made on a Panasonic NV-8050 time-lapse videorecorder using 1/4 in. 2 hr videocassettes. Twenty four hr recordings were made by setting the videorecorder to record 120 hrs on a single 2 hr cassette. This insured that any courtship and mating activities would not be missed. During periods of active courtship and mating, recordings were made at the 12 hr/cassette speed. This was done to increase temporal resolution.

III. OBSERVATIONS

First Recorded Mating

On 8 April 1983 and 6 min. into the dark cycle, the female No. 4 became active and was observed shifting her coils while in a crevice underneath a rock. Nine minutes later, the male No. 6, began crawling around the enclosure, tongue flicking repeatedly. No. 6 entered the crevice in which No. 4 was lying, still in a coiled position, 11 min. and 41 sec. after becoming active. At this time, No. 6 could be partially observed circling around No. 4's dorsum, tongue flicking while moving his head from left to right of No. 4's dorsal midline.

No. 6 left and, intensively tongue flicking, returned 2 min. later to the crevice which was occupied by No. 4. Upon his second return, No. 6 was seen circling around No. 4 under several rocks. Six minutes after No. 6's second return, No. 4 slowly crawled out from under the rock and was immediately followed by No. 6 who crawled up along her dorsum. Both snakes became partially hidden behind the rocks, although quivering as well as tail rattling could be seen in both snakes. Two minutes and ten seconds after No. 6 crawled up No. 4's dorsum, a sharp upward whip of No. 6's tail was observed. Nineteen seconds later the snakes were observed copulating with the female's tail above that of the male.

Two min. 38 sec. later, No. 4 started slowly crawling away, pulling the tail-rattling No. 6 along by his hemipenis. Although No. 6 made no attempt to maintain a position on top of No. 4, he would follow alongside her and would tongue flick and nose No. 4's dorsal side with his snout whenever No. 4 stopped. Often No. 4 would start crawling again after being "nosed" by the male. At one point, he approached her from behind a rock and apparently startled her, for she moved her head back with a jerk. No. 6 lifted his head to about a 45° angle with the substrate, exposing the very lightly colored ventral side of his head to the female for a period of 2 sec. No. 6 then lowered his head slightly and approached No. 4, stopping about 3 cm from her head. No. 6 then raised his head back to a 45 degree angle and retreated back around the rock separating the two snakes, only to reapproach No. 4 from behind with a low head-substrate angle.

The two snakes remained coupled for 4 hr 29 min. During this time No. 6 was by far the more active of the two. His anterior half remained in almost constant motion, while he displayed frequent tongue flicking. He also rattled his tail occasionally. Copulation ended in a barely noticeable movement in the two snakes' tails. Directly after hemipenal separation, No. 6 crawled and coiled up behind a rock. However, No. 4 now became very active, crawling around the enclosure for 1 hr 7 min.

Second Recorded Mating

On 21 April 1983, the large female (No. 1) was placed in the enclosure which already contained the male No. 6 and the female No. 4. This placement was made two hours into the dark cycle. Seven min. after being placed in the enclosure, No. 1 became active by reaching over from the rock on which she was placed to the water "pool." From this position she started drinking. While drinking, she was approached by No. 6, who had been lying coiled approximately 15 cm from her. The approach by No. 6 was accomplished by stretching the anterior quarter of his body upwards and outwards from a coiled posture. No. 6 tongue flicked No. 1's side intensely at about two head lengths caudal to No. 1's head-trunk juncture. No. 6 moved slightly posteriorly, still very actively tongue flicking, whereupon No. 1 raised her head above that of No. 6 for 1 min. 30 sec. Slight head bobbing was then seen in No. 1, but I was unable to tell whether these were simply drinking movements or signals of some sort elicited by No. 6. No. 1 once again lowered her

head to the water and No. 6 moved anteriorly to her all the while frequently tongue flicking at her (circa 20 tongue flicks/min.). No. 6's head vibrated with each flick of his tongue. He continued his approach until the top of his snout made contact with No. 1's side, whereupon, No. 1 jerked her head up and away from No. 6. No. 6 appeared completely undisturbed by this sudden movement and followed No. 1's highly raised and retreating head and anterior body. This high stance in No. 1 was maintained for 3 sec., after which she lowered her head slightly above her resting coils.

By this time, No. 1 had backed into the corner of the enclosure. She continued to jerk any segment of her body away from No. 6 when contact was made with his snout, until he reached her dorsum. At this point, No. 6 moved anteriorly down No. 1's partially coiled dorsum, tongue flicking at her while moving his head from left to right along her mid-dorsal line. This was continued until he reached the female's head. Here he paused 40 sec. and then crawled away from No. 1; he returned without stopping and once again circled around the dorsum of No. 1's coiled body, tongue flicking as described above. This circling around on top of No. 1, leaving, and returning was repeated three times. On the third instance, vigorous tail movements in No. 6 were observed. Two minutes later, intromission was confirmed with No. 1's tail above that of No. 6. This happened 36 min. after No. 6's original response to No. 1.

On several occasions after intromission first occurred, No. 6's tail was seen to spasmodically twitch at a rate of 2.2 twitches per

minute, which lasted around 8 min. No. 6's head and anterior body remained in almost constant motion during intromission. These movements looked similar to random searching movements associated with frequent tongue flicking. About one hour after copulation began, No. 1 started crawling away until about two thirds of her body had become uncoiled; she then stopped. No. 6 remained active around the posterior portion of No. 1 throughout the period of actual mating. Mating ended, 4 hrs 38 min. 7 sec. after it began, with a sharp jerk of the posterior third of No. 6's body. Directly thereafter he coiled up in the corner near where the mating had taken place. No. 1, on the contrary, gaped widely with her mouth and became very active crawling around the enclosure for the first time since the mating had begun. She remained active for 1 hr 46 min., not resting until the lights came on (see Table 10).

IV. DISCUSSION

Courtship and mating in the generally nocturnal crotaline snakes is little known, apparently due primarily to the lack of a suitable technique for observing the animals in the dark. Although Fitch (1960) did not actually see courtship and mating from start to finish in a captive copperhead (*Agkistrodon contortrix*) pair, he did manage a few glimpses by flashing a light into their cage at various times during the dark cycle. Using similar methods Antonio (1980) was able to observe courtship and mating in a pair of captive eyelash vipers (*Bothrops schlegeli*). Still Fitch was able to describe the female's

Table 10. Summary of behaviors seen during courtship and mating.

	08.04.83 Mating*	21.04.83 Mating**
Initial approach	male	male
Dorsal orientation	male	male
Body-jerking in response to contact with opposite sex	not observed	female
Time from initial approach to copulation	42 min., 15 sec.	35 min., 36 sec.
Male's tail looped under that of female's	yes	yes
Directive movements	female	female
Random movements	male	male
Tail-rattling	both	male
Tail-twitching during copulation	not observed	male
Tongue-flicking with head-vibration	male	male
Time snakes remained coupled	269 min., 0 sec.	278 min., 7 sec.
Active directly after copulation ended	female	female

*Mating between female No. 4 and male No. 6

**Mating between female No. 1 and male No. 6.

behavior towards the male as being more animated and jerky than usual, referring to the female's attempts to deter the male's approaches. This appears to differ from *C. rhodostoma* in that the female simply jerks portions of her body away from an advancing male instead of using what is apparently body-jerking to actively ward off the male. Still, possible individual differences cannot be excluded as all the studies above involved small sample sizes. In both the copperhead and eyelash viper, the male's tail was found to be looped under that of the female (Fitch, 1960; Antonio, 1980); I also found this to be true for *C. rhodostoma*.

Andren (1981) found both male and female adders (*Vipera berus*) tail rattle ("tail whipping" in Andren) just prior to copulation. *Calloselasma rhodostoma* performed this not only during courtship but during copulation as well. It occurred more frequently in the male than the female. This is in contrast to the findings in the adder in which no sex difference was found (Andren, 1981). Tail rattling has also been noted in male black ratsnakes (*Elaphe obsoleta*) during courtship (Noble, 1937), where it was believed to be associated with a high level of excitement. It should be noted that both black ratsnakes and *C. rhodostoma* are known to tail rattle when highly agitated (Pia York, personal communication; Hoesel, 1959). During courtship and mating it was most often seen in the male as he was being dragged around by the female or attempting to move in a direction opposite that of the female while attached by his hemipenis.

As in "Natrix-type" courtship (Davis, 1936), the female *C. rhodostoma* remains rather passive, with little relative movement as compared to that of the male, throughout the courtship-mating phase. Movement by the female was restricted to slight avoidance responses directed towards the male and temporally short "directive moves." I distinguish the "directive moves" of the female from male "random movements" in that "directive moves" lack all back-and-forth and to-and-fro movements of the anterior portion of the snake. "Random movements" seen in the male lack any apparent goal-directed movements, that is, any movements which would have the effect of directly bringing the snake from one locus to another. Instead, "random movements" appear to be constant meanderings of the anterior half of the snake only.

Other movements seen in the male snake, yet absent in the female, includes a form of dorsal orientation. This consists of the male positioning his ventral side on the dorsum of the female. This seems to be typical of serpent courtship and mating in general (Davis, 1936; Noble, 1937; Carpenter, 1977; Carpenter and Ferguson, 1977). Dorsal orientation in *C. rhodostoma* differs from that in the colubrids in the absence of caudocephalic waves and adpressed chin rubbing (Davis, 1936; Noble, 1937; Carpenter, 1977; Carpenter and Ferguson, 1977; Gillingham, 1979). What has been maintained, though, is the male's head movement from side to side along the mid-dorsal line of the female and the tongue flicking at the female's dorsum which usually accompanies it. This has been reported in *Storeria* (Noble, 1937).

A final note is that of the simultaneous occurrence of tongue flicking and head vibration. Andren (1981) found a close association between these two behaviors during courtship, where he referred to it as "intense flicking." It was noticed in *C. rhodostoma* during both courtship and mating as well as combat. This behavior occurred in bouts lasting as long as 30 sec., and consisted of intervals of less than a second during which the head rapidly vibrated, while the tongue was protruded. This was also frequently seen in conjunction with tail rattling. In that case the synchronized occurrence of tongue protrusion, head vibration and tail rattling created the impression that the sound given off by the rattling tail was coming from the snake's head. The potential of this behavior functioning as a signal during times of high excitation deserves further consideration.

CHAPTER V

NESTING AND BROODING

I. INTRODUCTION

Reptiles are not generally known for parental care of the eggs. In fact, the vast majority of oviparous reptiles abandon their eggs once they have been laid (Goin, Goin, and Zug, 1978). Still, one does find various reports of reptilian parental care in the form of egg-brooding (Vinegar, Hutchinson, and Dowling, 1970; Noble, 1935; Noble and Mason, 1933; Evans, 1959). The role that brooding plays appears to vary greatly among those reptiles in which this behavior is found. In the study by Noble and Mason (1933) on the brooding habits of several skink species of the genus *Eumeces* and the glass lizard *Ophisaurus*, it was found that female *Eumeces* actually rotate a large percentage of the eggs whenever she returns to the nest, much like one finds in birds; the exact function of this has yet to be investigated. It was further found that both *Eumeces fasciatus* and *E. laticeps* will actively defend their nest and eggs from both small and moderately sized mice, lizards, and snakes by not only attacking, but actually biting, the potential predator. This was in stark contrast to the shy *Ophisaurus*, who, although she brooded her eggs, retreated upon the slightest provocation. In this same study the possibility of heat transferral from the female to the eggs was raised for *Eumeces* after the

female had basked and returned to the eggs. This was found not to be so for *Ophisaurus*.

In Vinegar's (1968) study on the brooding habits of *Ophisaurus*, a temperature regulating function was shown. This is seen as being accomplished by the female changing the level of the eggs in the substrate in order to increase or decrease the temperature surrounding the eggs. Maternal care of the eggs is carried even further by *Eumeces obsoletus* which is known to aid the young during hatching by stimulating them to move spasmodically, thus aiding them to escape the shell (Evans, 1959).

Noble (1935) reported on egg brooding for various elapids (*Naja naja, Ophiophagus* (=*Naja*) *hannah, Bungarus ceylonicus, B. fasciatus*) and a few viperids (*Trimeresurus monticola, Calloselasma* (=*Trimeresurus*) *rhodostoma,* and *Lachesis mutus*). Brooding is also well known in several of the boids including *Morelia spilotes, Python curtus, P. reticulatus, P. sebae, P. molurus,* and *Chondropython virdis* (Vinegar, Hutchison, and Dowling, 1970). Other snakes occasionally observed to brood eggs include the burrowing worm snakes, *Leptotyphlops* (Bellairs, 1970), the black ratsnake, *Elaphe o. obsoleta*, and the mud snake, *Farancia abacura* (Oliver, 1955). The black ratsnake reported by Oliver (1955) was observed basking in the sun and returning to the nest to coil around the eggs. This method of raising the temperature of the eggs by the female behaviorally raising her own body temperature through basking and returning to the eggs has also been observed in *Morelia spilotes*, the Carpet python (Cogger and Holmes, 1960; cited in Vinegar, Hutchison,

and Dowling, 1970). Physiological thermoregulation during brooding has been shown for *Python molurus bivittatus* (Hutchison, Dowling, and Vinegar, 1966), *Python curtus*, and *Chondropython viridis* (Vinegar, Hutchison, and Dowling, 1970).

In the king cobra (*Ophiophagus hannah*) it was observed that the presence of the female in the nest had no effect on the temperature that would aid in the incubation of the eggs, but her presence in the nest was for protection of the eggs only (Oliver, 1956). This idea of the brooding female protecting the eggs is also seen in the viperine snake *Trimeresurus monticola*, which Pope (1935:415) found to be ". . . rather sluggish and disinclined to strike except when guarding eggs." Noble (1935) also saw the protection of the eggs provided by the brooding female as being to the advantage of the species with or without physiological or behavioral thermoregulation.

II. MATERIALS AND METHODS

In order to test the hypothesis that brooding in *C. rhodostoma* was having an effect on the temperature of the eggs; data on the egg, air, and substrate temperatures were collected. All six snakes were housed together in the 90 × 60 × 60 cm wooden enclosure fitted with a glass top and front side. The two smaller males (Nos. 5 and 6) were removed from the enclosure on 27 April 1982 and on 13 May 1982 the only remaining male in the enclosure (No. 2) was killed (see above).

Temperature readings during brooding by No. 1 were obtained from 3 thermocouples each connected to a YSI Model 4002 switch box, which

was in turn connected to a YSI tele-thermometer. Both the switch box and tele-thermometer were outside of, but next to the enclosure. Prior to the placement of the thermocouples in the enclosure, each was calibrated and compared to the others according to the instructions specified by the manufacturer. This was done in order to assure comparable recordings between the three thermocouples. Simultaneous temperature recordings were taken for air, substrate, and clutch. Air temperature was obtained by a thermocouple hanging 15 cm above the brooding female (No. 1). Substrate temperature was taken from a thermocouple 10 cm in front of No. 1, while the clutch temperature was recorded from a thermocouple placed between the coils of No. 1 and her eggs. Several temperature recordings were made daily for the 26 day period extending from 10 September 1982 until 6 October 1982. Recordings were generally made during the dark cycle between 0800 and 1830 EST. In addition, temperatures were taken every 15 minutes from 2030 EST on 19 September 1982 until 0800 EST on 20 September 1982 and again from 0815 until 2015 EST on 21 September 1982. This gave a continuous 24 hour sampling of changes in temperature.

Data on the brooding female's response to changing levels of humidity were obtained by positioning an Abbeon Relative Humidity/Temperature Indicator (Model M2A4) 22 cm directly above the female. This, too, was calibrated prior to its installation according to the manufacturer's instructions. A Sony black and white video camera placed in front of the enclosure was focused on the hygrometer, and another Sony black and white video camera was hung above the enclosure with its film plane

parallel to the floor of the enclosure. The latter camera was focused on the brooding female. Through the use of the Sony Special-Effects-Generator, a single picture image was produced such that simultaneous recording from both cameras was possible. Care was taken such that the image of the hygrometer would not interfere with the image of the brooding snake. Twelve-hour video recordings were made during the dark cycle, and egg and humidity data were taken from these tapes, which were recorded over a period extending from 8 September till 16 September 1982. The data consisted of 189 egg-humidity comparisons made at one-half hour intervals. Data for the number of eggs were determined by projecting the video image on a 5-1/4 in. diagonal black and white monitor screen equipped with a grid divided into 1/8 in. squares and counting the number of squares in which eggs were showing.

III. RESULTS

Temperature

A Friedman nonparametric test of differences between means was run on the temperature data. A rank of 1.44 was found for the substrate temperature and a rank of 2.28 was found for both the air and clutch temperatures. The substrate temperature ranked significantly lower than that of both clutch and air ($\chi^2 = 71.7$, df = 2, $p < 0.0001$). The means and ranges of the temperature data are shown in Fig. 5. In addition, three separate paired t-tests were run in order to obtain a more complete picture of differences between the three temperature means. The results are summarized in Table 11. The mean substrate temperature is significantly different from that of both the mean clutch

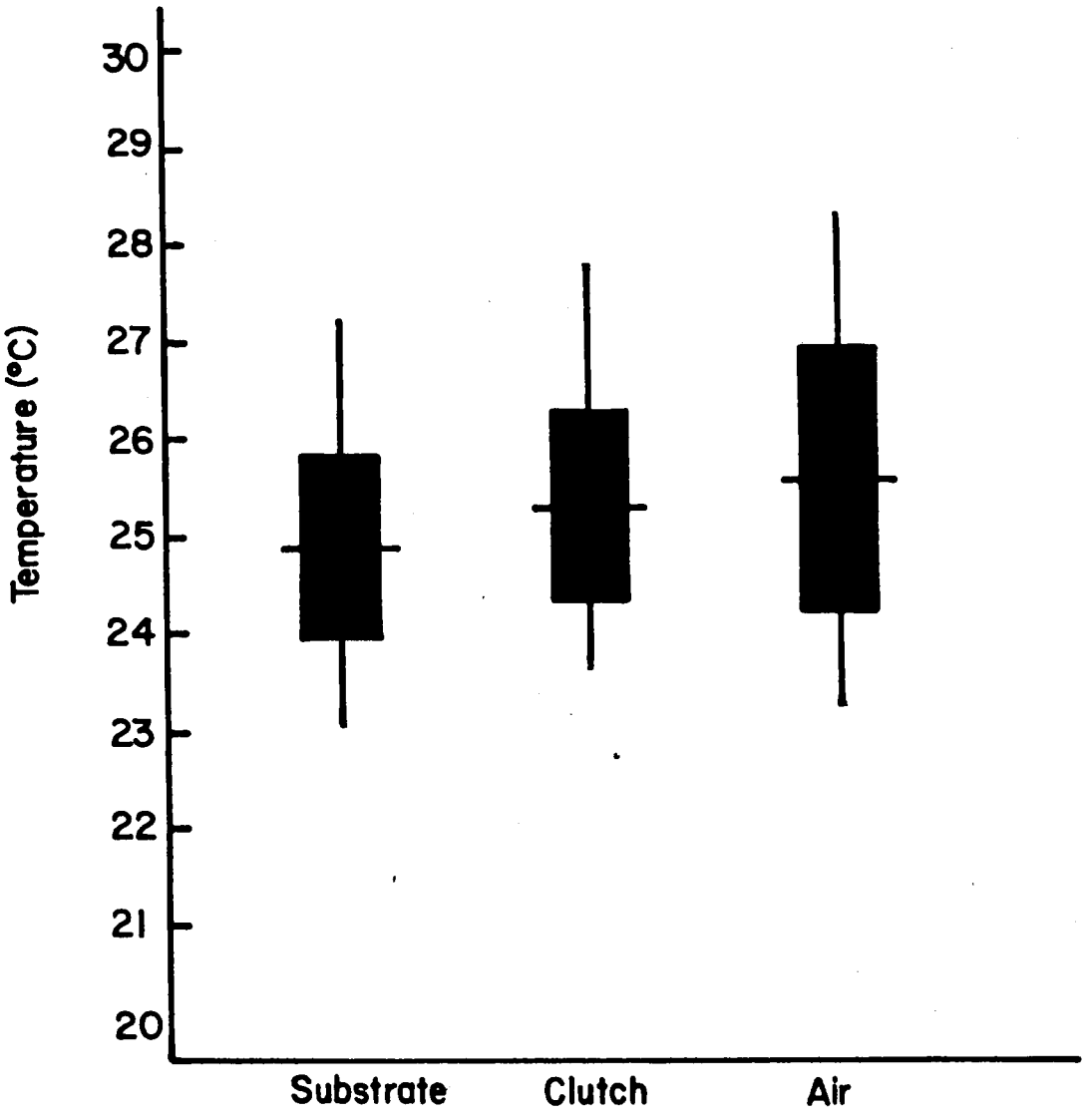


Fig. 5. Temperatures of substrate, clutch, and air during brooding in *Calloselasma rhodostoma*. Horizontal line represents the mean; solid rectangle one standard deviation on either side of the mean; vertical line the range. N = 153.

Table 11. T-tests of Ho: temperature A = temperature B; for simultaneous temperatures recorded during brooding in *Calloselasma rhodostoma*.

Variable	Mean (°C)	t-value	df	p<
Substrate Eggs	24.90 25.29	-10.45	152	0.0001
Substrate Air	24.90 25.39	- 7.66	152	0.0001
Eggs Air	25.29 25.39	- 1.45	152	0.149

and air temperatures, but the mean clutch temperature is not significantly different ($p < 0.05$—two-tailed) from that of air.

Changes of temperatures and between temperatures taken for the substrate, clutch, and air over a 24 hour period is graphically depicted in Fig. 6. Data points were obtained by averaging four consecutive temperature readings taken simultaneously at fifteen minute intervals from each thermocouple.

Humidity

Data were collected for the amount of egg area showing and compared to the percent relative humidity. As the enclosure was kept damp by several daily sprayings of water, a large percentage of the collected data was for a humidity level of 100%. This resulted in a truncated model with a very large degree of variance in the amount of eggs showing at 100% relative humidity; for this reason all data taken at 100% relative humidity were deleted from the data set before attempting to fit a regression model. It should also be noted that such high humidity readings were often associated with the disturbance involved in spraying the inside of the enclosure.

Several regression models were run for the entire data set minus the data at 100% relative humidity. The amount of egg area exposed was the dependent variable. Although several significant models were found ($p < 0.0001$), a plot of residuals around the regression line indicated that they were poor models. Log 10 transformations carried out on the data did not improve the model. The data were then divided

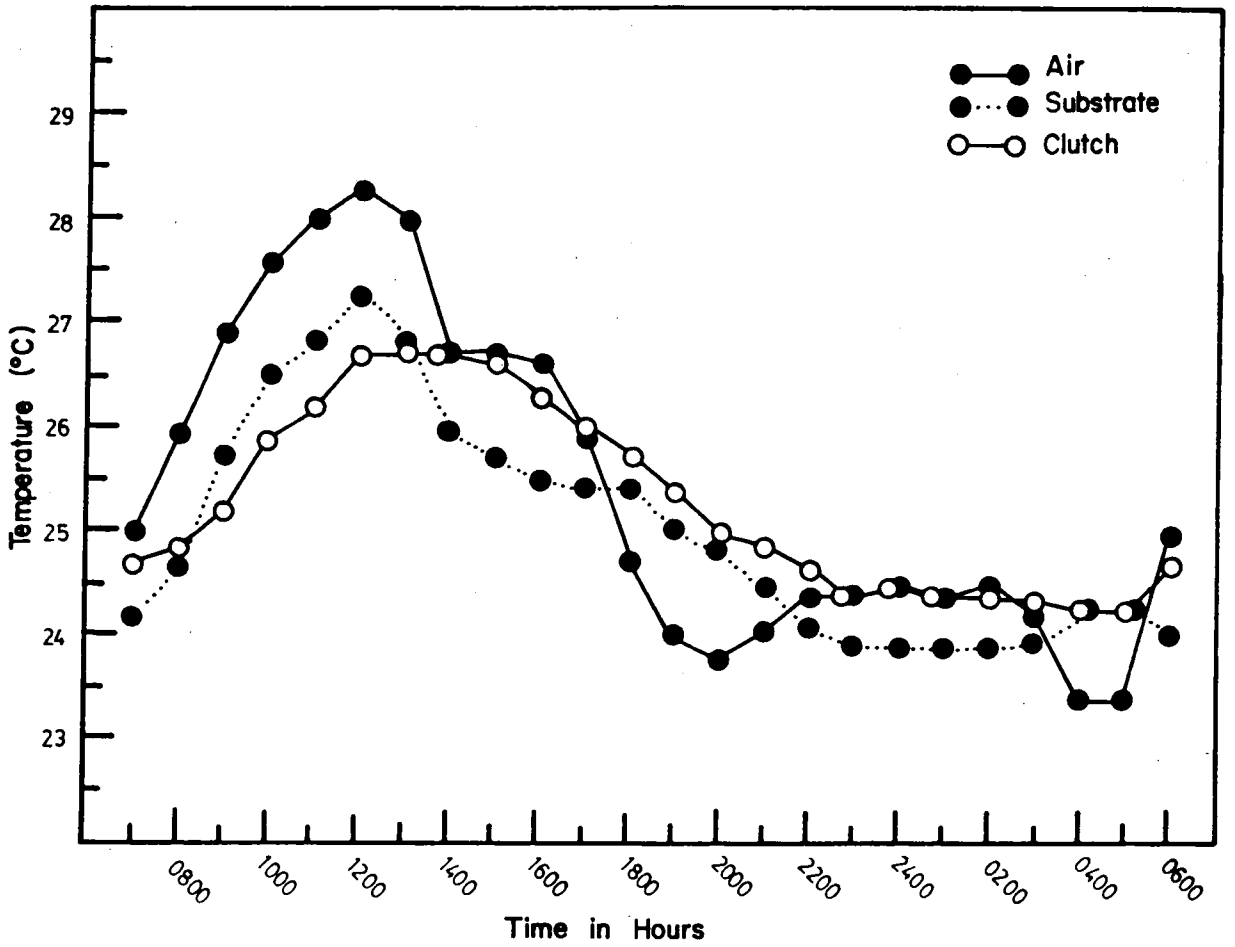


Fig. 6. Temperature changes over a 24 hr period during brooding in *Calloselasma rhodostoma*. Data points represent averages over 4 temperature readings taken at 15 min. intervals.

up into two sets. One set consisted of humidity data for humidity ranging from 60% to 83%, and another set for humidity ranging from 86% to 99%. Regression models were run for both sets. The best fit was accomplished with a second degree polynomial model ($F = 52.5$, $df = 2.44$, $p < 0.0001$) fitted to the lower humidity set. A significant ($p < 0.05$) model could not be fitted to the higher humidity set (Fig. 7).

IV. DISCUSSION

From the temperature data it does not appear that brooding in *C. rhodostoma* is having any effect on the subsequent temperature of the clutch other than in decreasing its overall daily temperature variation. This temperature stabilizing effect could be expected from any large covering body. It has been shown that a brooding female Indian python (*Python molurus bivittatus*) is capable of maintaining body temperatures as much as 7.3°C above that of either the substrate or ambient (air) temperature for extended periods of time. It was further shown that the animal was able to do this by means of spasmodic contractions of the body musculature, which had the result of increasing both the metabolism and body temperature (Hutchison, Dowling, and Vinegar, 1966; Vinegar, Hutchison, and Dowling, 1970). Hutchison, Dowling, and Vinegar (1966) were able to determine that for the python 33°C could be considered analogous to the "lower critical temperature" of birds and mammals; that is, the brooding animal only began to increase its rate of oxygen consumption once the ambient temperature was lowered below 33°C.

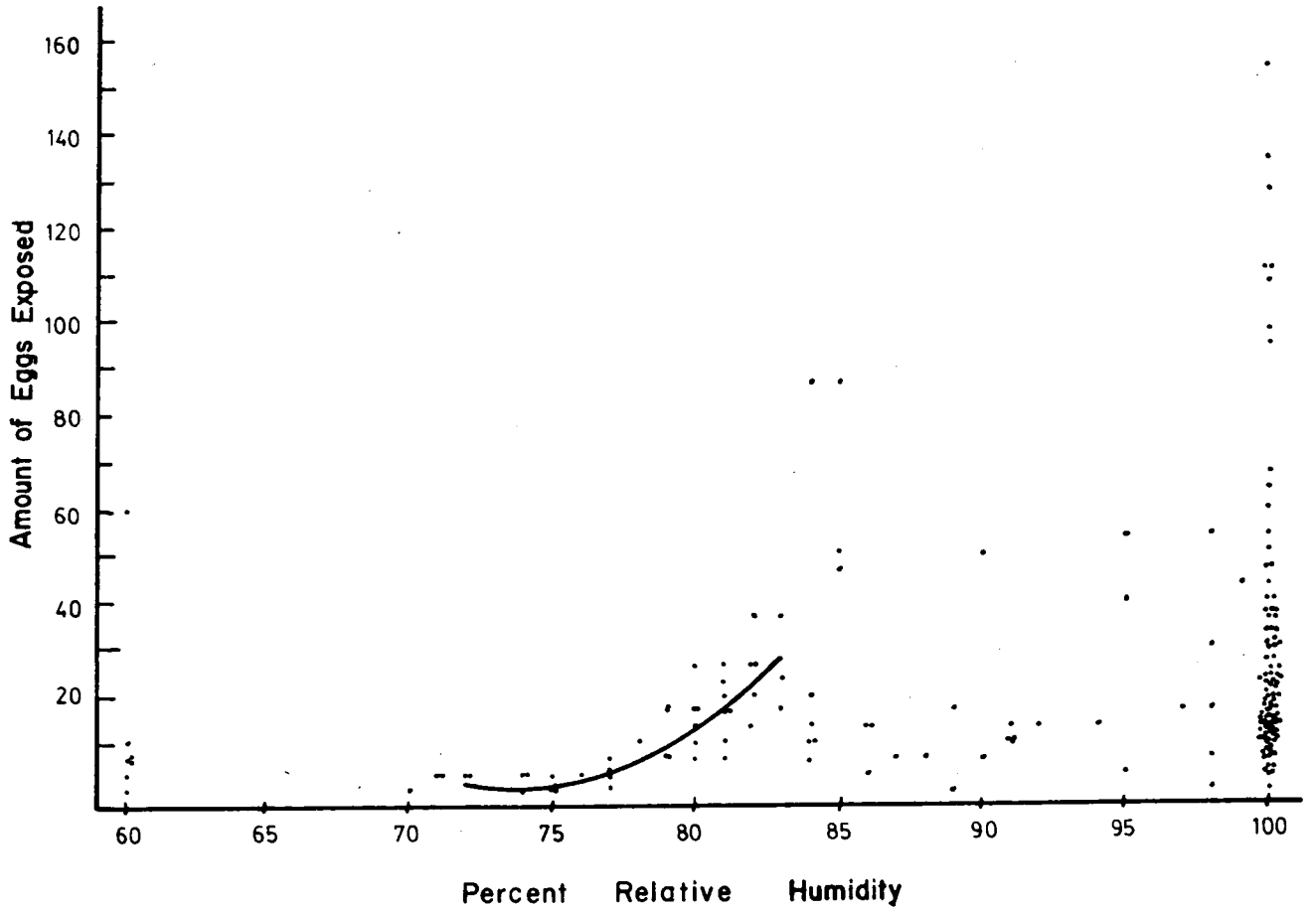


Fig. 7. Amount of eggs exposed (= No. of grids with eggs showing on monitor) regressed on the percent relative humidity. Data were collected during brooding in *Calloselasma rhodostoma*.

In *C. rhodostoma* the body temperature of the brooding female during the 24 hr sample was above that of the ambient (air) temperature over a period of around nine hours (see Fig. 6, p. 65). This occurred during a steep decline in the air temperature after it had reached its peak at 0200 hrs. During this period the maximum air-clutch temperature deviation was only 1.4°C. Although one could hypothesize a "lower critical temperature" for brooding in *C. rhodostoma* to be 24°C, tests in which the ambient temperature would be lowered below 24°C for extended periods of time would be necessary, and this could have serious detrimental effects on embryo survival (Vinegar, 1973). The results presented in Table 11, p. 63, further substantiate the finding of no overall increase in clutch temperature during brooding.

It should also be noted that as the majority of the temperature data were obtained during the cooler dark cycle, they were biased towards warmer body temperatures with respect to the ambient temperature. Vinegar, Hutchison, and Dowling (1970) felt that the fact that *Python reticulatus* did not incubate its eggs was limiting its northerly distribution (circa 22° N. Lat.), whereas *Python molurus* with its ability to increase its body temperature during brooding allowed it to extend its range up into Southern China (circa 27° N. Lat.). In contrast, the range of *C. rhodostoma* probably does not extend much further than Phitsanulck, Thailand (16.5° N. Lat.); a range which is more comparable to that of *P. reticulatus*. From Fig. 8 is can be seen that the mean temperature of a ten year period for the northerly part of its range is 28.3°C during its most likely laying period.

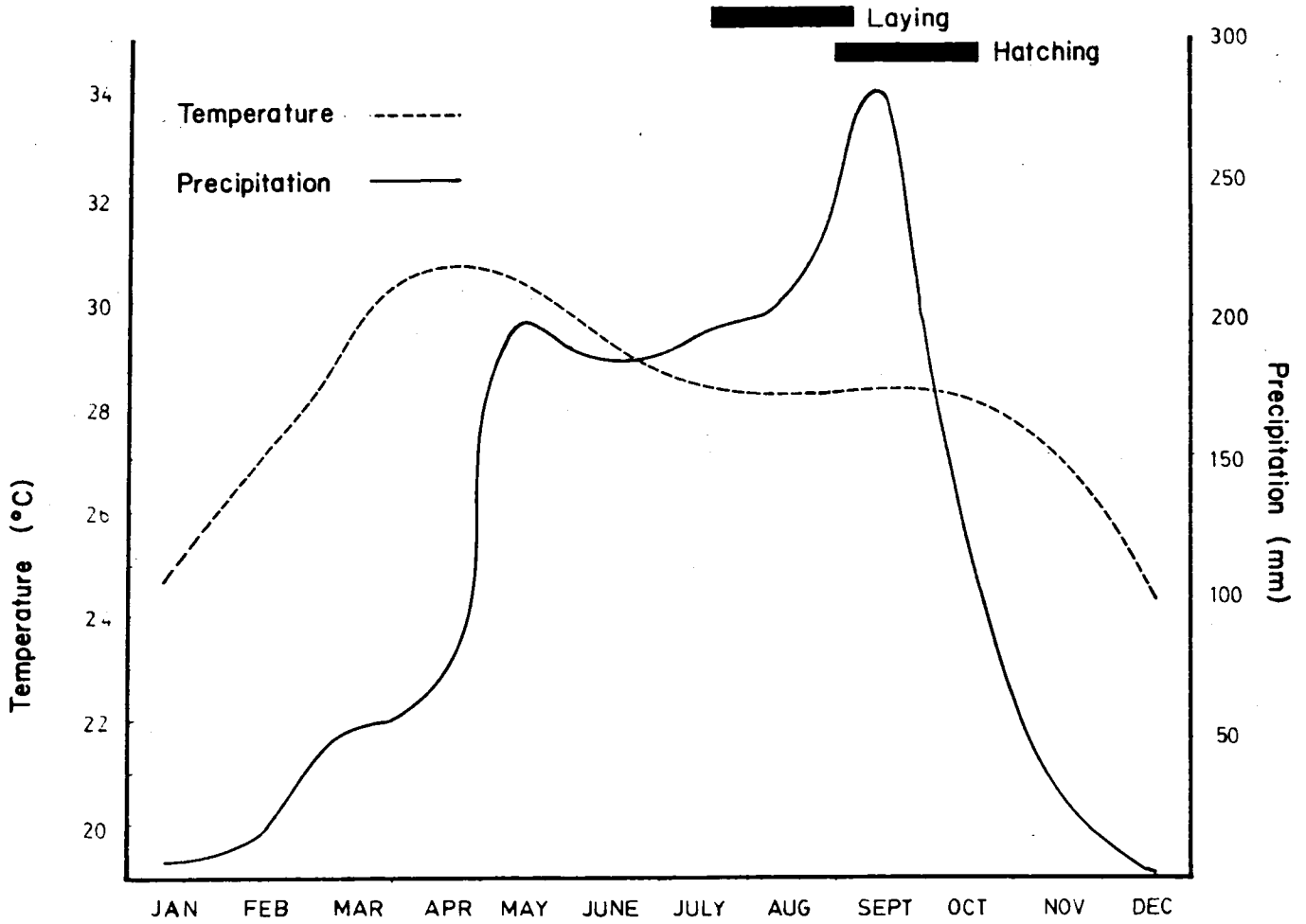


Fig. 8. Temperature and precipitation averages for a 10 yr period at the Phitanulok, Thailand, weather station (16.50 N. Lat.) and approximate egg laying and hatching times for *Calloselasma rhodostoma*. (Weather information obtained from the U.S. Dept. Commerce, Environmental Sci. Services Admin., Environmental Data Service. World Weather Records 1950-60, Vol. 4, Asia.)

Bellairs (1970) mentions the possibility that brooding in reptiles might protect the eggs from chilling breezes, though in *C. rhodostoma* its forested habitat would lessen this effect somewhat.

The outer covering of the eggs of oviparous snakes is a calcium impregnated fibrous membrane, which allows them to be laid on land. Although the egg's membranes reduce desiccation, oviparous reptiles must be careful in selecting a proper nesting site, as appropriate heat and moisture are of the utmost importance in assuring the proper development of the embryos. Goin, Goin, and Zug (1978) believe that, in general, reptiles must show greater care in selecting sites to nest for their eggs than most amphibians. Adaptation to the problem of desiccation of the porously membraned eggs can be seen in the habit of many terrapins of moistening the nest with urine. The European terrapin (*Emys orbicularis*) has been observed to drink water when laying during hot weather in order to replenish her cloacal bladders with fluid with which to moisten her nest and eggs (Bellairs, 1970).

The importance of humidity in the development of the eggs in *Python sebae* was shwon by Joshi (1967, cited in Vinegar, Hutchison, and Dowling, 1970). He divided a single clutch into various groups of eggs, each receiving either 65 to 80% relative humidity at 22.2°C to 28.9°C, 80 to 90% relative humidity at 30.0° to 32.2°C or less than 40% relative humidity at 21.1 to 32.2% relative humidity. He found that the groups kept at 65 to 80% relative humidity and 80 to 90% relative humidity hatched, whereas the group kept below 40% relative humidity failed to hatch.

The results of the observations of a brooding female *C. rhodostoma* at various percentages of relative humidity showed a significant negative correlation between the amount of egg exposure and the ambient humidity level (measured as a percent relative humidity) between 69 and 83% relative humidity. Above 83% the correlation decomposed as a result of the tremendous variation in the amount of egg exposure. Often, after the humidity had decreased below 70%, the female would have the eggs completely covered with no egg exposure. After the enclosure with the brooding female was sprayed thoroughly, the relative humidity would immediately increase to 100%. The female's initial response to this was a loosening of the coils increasing greatly the amount of egg exposure. On several occasions, the relative humidity level remained at or near 100% for a period of several hours. When this occurred, the female's initial response of loosening her coils and thereby increasing the egg exposure would be followed by a decrease in egg exposure by tightening her coils. This had the overall effect of increasing greatly the variance in the data during extended periods of high humidity.

From these data it is difficult to determine exactly what the brooding female is responding to, but humidity may be only one of several factors determining egg exposure. One such factor might be egg turgidity, on which humidity could very well be playing a role. In such a case the following two factor sequence of events determining egg exposure could be postulated: humidity high, egg turgidity low, then expose eggs; or humidity low, egg turgidity low (or decreasing),

then cover eggs. In the tropics, where humidity levels are generally high, especially in forested areas, changes in humidity might be more critical to the survival of the developing eggs. In Singapore humidity has been shown to fluctuate as much as 22 percentage points of relative humidity (Lockwood, 1974). As the time of laying appears to occur during the period of greatest rainfall, it can be imagined that any deviations from this high precipitation level could have serious consequences on the eggs (Fig. 8, p. 69).

It has been assumed for some time that a major role of brooding in snakes is the protection it gives the eggs, although little direct evidence for this hypothesis can be found in the literature. Oliver (1956) was unable to find a temperature difference between the brooded eggs and the ambient temperature in the king cobra (*Ophiophagus hannah*) and so concluded that brooding in this snake must be providing protection. Still, he found that the female is more concerned with covering the eggs (humidity maintenance?) than in driving off a potential predator. Noble (1935), after determining that certain female lizards shown to brood their eggs will actively defend their eggs from predatory attacks, concluded that the same must be true for the majority of brooding snakes as it would be to the advantage of the species with or without physiological thermoregulation.

In my own observations on brooding in *C. rhodostoma*, I found the brooding female to actively defend the nest by means of body-jerking. This same behavior was observed by Finstrom (unpublished manuscript). This action appears to be similar if no identical to

"body-jerking" described by Carpenter and Gillingham (1975), as a defensive response exhibited by crotaline snakes in response to kingsnakes, which are known to be ophiophagous. In *C. rhodostoma*, body-jerking was seen as a jab of a short segment of the trunk directed against some intruding object with the effect of forcing the object away from the snake. This response could be elicited by an inanimate object such as a snake hook as well as a conspecific. When body-jerking was directed against a conspecific, the initial reaction of the latter was a startle response, whereby the intruder would freeze for as long as three minutes. The body-jerking response disappeared two days after hatching of the neonates, who did elicit the body-jerking response.

In one case the intruding conspecific was a female which proved to be gravid. This is interesting as the gravid female (No. 3) was very persistent in its attempts to coil atop the already brooding female (No. 1). These attempts were first observed on 3 September 1982, 27 days after No. 1 had laid the eggs. On 7 September 1982, No. 3 was successful in gaining a position on top of No. 1 and her eggs. No. 3 was removed from the enclosure and was isolated in a small, separate terrarium. It was discovered on 19 September 1982 that No. 3 had also laid eggs and was observed coiled tightly around them. On that same day, No. 3 was lifted off her nest so that the eggs could be weighed and measured. When lifted off the eggs, No. 3 exhibited body-jerking to the snake hook typical of that seen in No. 1. Once the eggs were returned along with No. 3, no body-jerking was observed

in response to light jabs from a snake hook. Furthermore, No. 3 refused to coil around the eggs which had been replaced in the same spot where they were found. After three days, the eggs had to be removed in order to enhance their chances for survival. The reason for No. 3's refusal to brood her eggs after weighing and measuring remains unknown (all handling of the eggs was carried out with the use of clean plastic gloves).

One final note on defense of eggs from a brooding female is that of passive defense given by the camouflaging coloration of the brooding female. As the eggs are laid on top of the substrate floor, they would be very visible to a predator due to their highly reflective white surface, but once covered by the brooding female they disappear under her body, whose color and patterns blend in well with the ground.

CHAPTER VI

CONCLUSIONS

Students of reptile behavior have for too long ignored the fact that many of their species are nocturnal or crepuscular; a lack of concern for the animal's daily activity cycle can have detrimental effects on the investigation. In this thesis, I used a simple reversed cycle red light technique to observe the nocturnal habits of *Calloselasma rhodostoma*. My eyes became acclimated to the red lit scotophase in only one or two minutes; after which direct observations could be readily made. I also found that, with the proper adjustments, sharp pictures could be recorded on videotape. Thus I was able to use two of the most important methods used by ethologists, direct observation and analyses of visually recorded behavior.

The response of *C. rhodostoma* to the onset of red lighting during the scotophase was to become active. The interactions observed between the snakes (male combat, courtship and mating) appeared very similar to descriptions of the same activities seen in the field in related snake species. Thus, it is safe to say that the behaviors of *C. rhodostoma* in a captive, red-lit environment do not vary greatly from the nocturnal behaviors of this snake in the field.

The behavioral categories used in analyzing combat varied only slightly from the categories of other researchers working with viperid combat (Carpenter, Gillingham, and Murphy, 1976; Andren, 1981). The

ethogram developed in this study provided both accurate and high resolution of the behavioral transitions during combat. While it is unfortunate that only two complete combat sequences (involving just two individuals) could be analyzed, I feel the groundwork has been laid for a more extensive investigation of combat in *C. rhodostoma*. The use of a larger sample size, both in number of individuals and combat sequences, would greatly facilitate the subsequent analysis of combat.

The first unobtrusive recordings of courtship and mating sequences in a crotaline snake during the scotophase were made. Previous reports of nocturnal courtship and mating in crotalines involved the use of flashlights which was reported to have had a disturbing effect on the animals (Fitch, 1960; Antonio, 1980).

The observations of combat as well as that of courtship and mating occurring under the illumination of red lights are two examples of the applicability and usefulness of the nocturnal surveillance methods used in this thesis. *Calloselasma rhodostoma* also proved to be an invaluable and cooperative subject for behavioral research on captive animals. Still, there remains a substantial gap in our knowledge of the behavior of the many nocturnal reptiles. I therefore feel that expanding the techniques used in this thesis to the many other nocturnal reptiles will provide much information on the behavior and energetic of reptiles in general.

Finally, I showed that, during brooding, *C. rhodostoma* responds to stimuli arising from changes in the level of relative humidity. These

behavioral responses most likely affect the amount of moisture the clutch receives. The importance of proper levels of moisture for the survival of the porous, membraned eggs of reptiles is well-known (Bellairs, 1970; Goin, Goin, and Zug, 1978), but until now, no one has indicated behavioral regulation of the moisture content of eggs by a brooding female. I have found a strong indication that *C. rhodostoma* is regulating the moisture content of the eggs during brooding by varying the amount of exposure the clutch receives at different humidity levels. I also feel that the regulation of the moisture content of the eggs may be an important role in brooding in other reptiles as well.

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APPENDICES

APPENDIX A

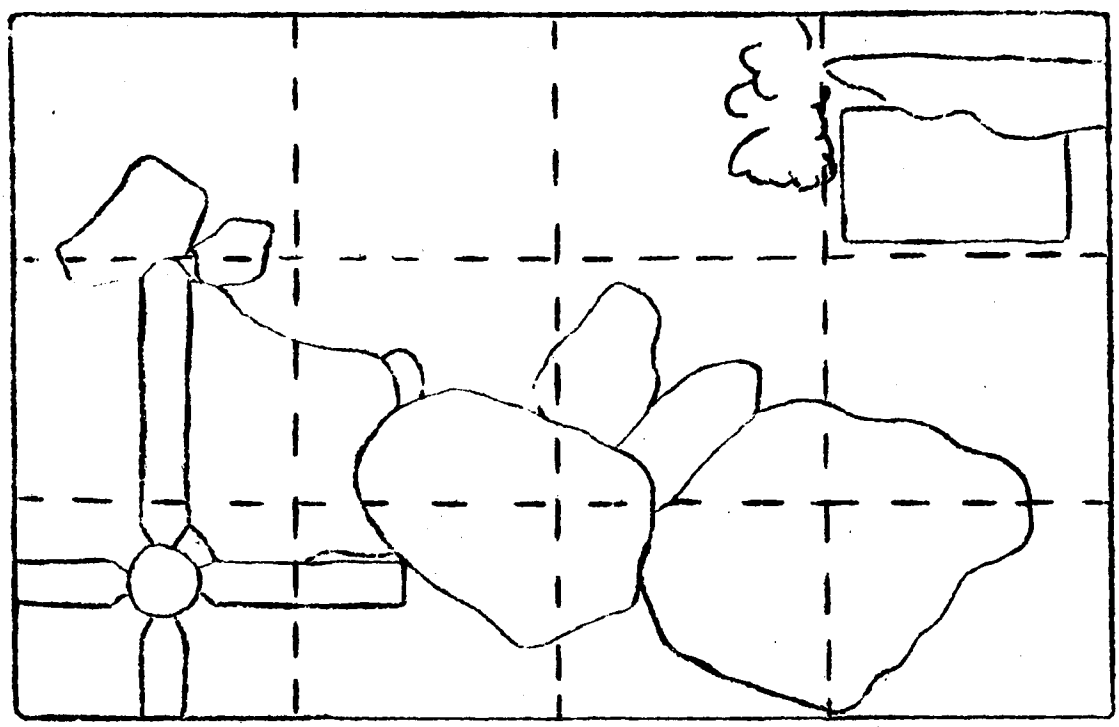
DAILY OBSERVATION SHEET USED FOR RECORDING MAINTENANCE AND ACTIVITIES OF *CALLOSELASMA RHODOSTOMA*

DATE: _____ FOOD: _____

TIME: _____ _____

OBSERVER: _____ OTHER: _____

FRONT



OBSERVATIONS/COMMENTS:

% REL. HUMIDITY: _____

TEMPERATURE: _____

APPENDIX B

SNAKE SPECIES KNOWN TO COMBAT

BOIDAE	
Morelia spilotes	Covacevich, 1975 (cited in Shine, 1978)
Pyton molurus	Barker, Murphy, and Smith, 1979
Sanzinia madagascariensis	Carpenter, Murphy, and Mitchell, 1978
COLUBRIDAE	
Coluber constrictor	Shaw, 1951
Coluber gemonensis	Bogert and Roth, 1966
Coronella austriaca	Bogert and Roth, 1966
Drymarchon corais	Shaw, 1951
Elaphe guttata	Shaw, 1951
Elaphe longissma	Stemmler-Morath, 1935 (cited in Shaw, 1951)
Elaphe obsoleta	Brecke, Murphy, and Seifert, 1976
Elaphe quadrivirgata	Shine, 1978
Lampropeltis calligaster	Moehn, 1967
Lampropeltis doliata	Shaw, 1951
Lampropeltis getulus	Murphy, Tryon, and Brecke, 1978
Lampropeltis mexicana	Murphy, Tryon, and Brecke, 1978
Lampropeltis triangulum	Shine, 1978
Malpolon monspessulanus	Bogert and Roth, 1966
Masticophis taeniatus	Bennion and Parker, 1976
Pituophis melanoleucus	Shaw, 1951
Psammophis punctulatus	Pitman, 1974
Pseudaspis cana	Shine, 1978
Ptyas mucosus	Shaw, 1951
Sonora episcopa	Kroll, 1971
ELAPIDAE	
Bungarus candidus	Shine, 1978
Dendroaspis jamesoni	Leloup, 1964
Dendroaspis polylepis	Leloup, 1964
Dendroaspis viridis	Dan MacDonald (personal communication)
Naja haje	Shine, 1978
Naja naja	Shine, 1978
Naja tripudians	Shine, 1978
Ophiophagus hannah	Oliver, 1956
Oxyuranus scutellatus	Worrell, 1963 (cited in Carpenter and Ferguson, 1977)

Notechis ascutatus	Shine, 1978
Pseudecis porphyriacus	Shaw, 1951
Pseudonaja textilis	Shaw, 1951

VIPERIDAE (CROTALINAE)

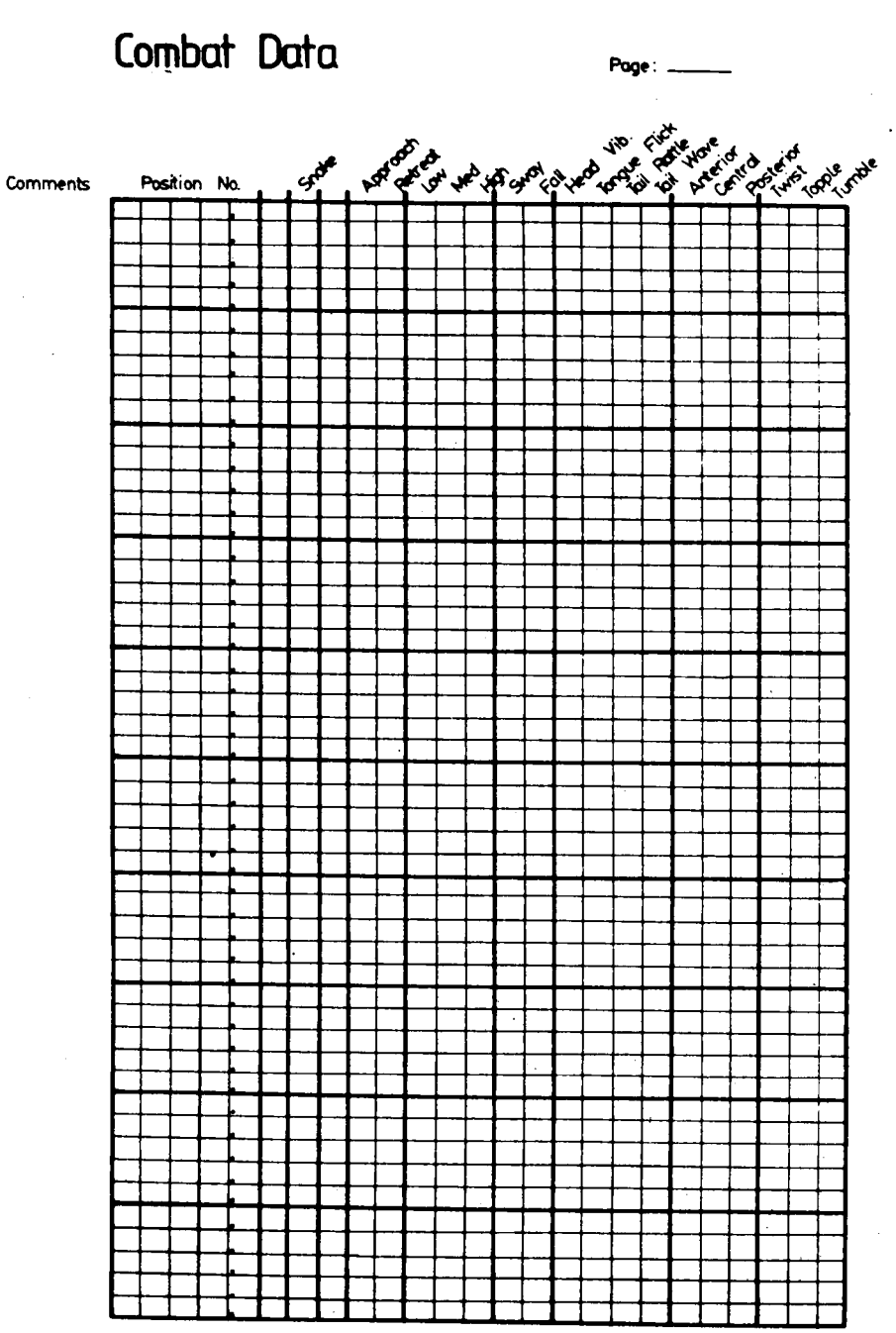
Agkistrodon bilineatus	Burchfield, 1982
Agkistrodon contortrix	Gloyd, 1947
Agkistrodon piscivorus	Perry, 1978
Calloselasma rhodostoma	personal observation
Crotalus adamanteus	Sutherland, 1958
Crotalus atrox	Klauber, 1972
Crotalus cerastes	Lowe and Norris, 1950
Crotalus durrissus	de Langlada, 1975
Crotalus horridus	Klauber, 1972
Crotalus lepidus	Carpenter, Gillingham, and Murphy, 1976
Crotalus mitchelli	Klauber, 1972
Crotalus ruber	Klauber, 1972
Crotalus scutulatus	Shine, 1978
Crotalus viridis	Klauber, 1972
Sistrurus miliarus	Palmer and Williamson, 1971 (cited in Shine, 1978)

VIPERIDAE (VIPERINAE)

Bitis arietans	Thomas, 1972 (cited in Bennion and Parker, 1976)
Causus defilippi	Pitman, 1974
Causus lichtensteini	Pitman, 1974
Causus resimus	Pitman, 1974
Vipera ammodytes	Pitman, 1974
Vipera aspis	Thomas, 1969 (cited in Bennion and Parker, 1976)
Vipera aspis	Bogert and Roth, 1966
Vipera berus	Andren, 1981
Vipera latastei	Trutnau, 1975
Vipera lebetina	Stemmler, 1967 (cited in Bennion and Parker, 1976)

APPENDIX C

DATA SHEET USED IN RECORDING BEHAVIORAL TRANSITIONS DURING COMBAT IN *CALLOSELASMA RHODOSTOMA*



APPENDIX D

COMPUTER ROUTINE USED IN ANALYZING COMBAT IN *CALLOSELASMA RHODOSTOMA*

A computer routine was developed by Paul Wright (The University of Tennessee Computer Center) and myself for use on the SAS software package. This routine, while producing a large data set, requires a minimum of data to be transcribed from the recorded medium (e.g., videotape).

The procedure for collecting data involved recording any change in the behavioral categories being scored. This meant recording the time (on video tape, the recorded time from the time-date generator at the moment of change), the subject in which the behavioral change occurred, and scoring a "1" for the onset of a particular behavior or a "0" at the time the behavior ceased. All other behavioral categories for the individual being scored would likewise be scored as either occurring, "1," or not, "0," at that particular instant in time.

For an example, let us say, at 1 min., 58 sec., snake "A" is crawling (=behavior "X") around the enclosure with its head low to the substrate (=behavior "Y"). At 2 min., 42 sec., snake "A," while still crawling (=behavior "X"), raises its head (=behavior "Z"; behavior "Y" ceases). At the start of recording (1 min., 58 sec.), snake "B" has been peaceably lying coiled with its head low on the substrate. This sequence of behaviors would be scored on the data sheet as follows:

MIN.	SEC.	SNAKE	X	Y	Z
001	58	B	0	1	0
001	58	A	1	1	0
002	42	A	1	0	1

These data would then be recorded on a computer data set and run through the SAS routine shown here. This would produce a new data set consisting of 44 consecutive, one sec. intervals containing the scores for the three behavioral categories for snakes "A" and "B." The form of this data set is shown below:

TIME	AX	AY	AZ	BX	BY	BZ
118	1	1	0	0	1	0
119	1	1	0	0	1	0
120	1	1	0	0	1	0
.	.	.	.	.	.	.
.	.	.	.	.	.	.
.	.	.	.	.	.	.
161	1	1	0	0	1	0
162	1	0	1	0	1	0

Here, TIME is the converted time in seconds, and AX, AY, AZ, BX, BY, BZ represent the behavioral categories X, Y, Z for snakes A and B, respectively.

The output from the PROC step would consist of 36 2×2^{2} tables of association between each of the 3 behavioral categories in one snake at one interval (=1 sec.) preceding each of the 3 behavioral categories of the other snake. The information from these tables can then be summarized in two sociomatric matrices for "acts preceding" and "acts following" for each snake.

It should be noted that this routine is very flexible. Intra-individual paired associations can be made by changing the variables in

the TABLES statement under the PROC step. In the case of intra-individual paired associations one must be careful that the assumption of mutual exclusivity between the paired categories is maintained.

SAS COMPUTER CODE

```
DATA COMBAT;
INPUT MIN 1-3 SEC 4-5 SNAKE $ 7 X 9 Y 10 Z 11;
PRE_X=LAG1(X);
PRE_Y=LAG1(Y);
PRE_Z=LAG1(Z);
CARDS;

(data set here)

DATA A; SET COMBAT; IF SNAKE=A;
TIME=60*MIN + SEC;
AX=X;
AY=Y;
AZ=Z;
PRE_AX=PRE_X;
PRE_AY=PRE_Y;
PRE_AZ=PRE_Z;
KEEP TIME AX AY AZ PRE_AX PRE_ZY PRE_AZ;
DATA B; SET COMBAT; IF SNAKE=B;
TIME=60*MIN + SEC;
BX=X;
BY=Y;
BZ=Z;
PRE_BX=X
PRE_BY=Y
PRE_BZ=Z
KEEP TIME BX BY BZ PRE_BX PRE_BY PRE_BZ;
MACRO SPREAD
DATA DDD;
DO I=1 TO (NNN - 1);
J=I + 1;
SET DDD NOBS=NNN POINT=J; T2=TIME;
SET DDD POINT=I; T1=TIME;
DO T=T1 TO (T2-1) BY 1; OUTPUT; END;
DROP T1 T2 TIME;
RENAME T=TIME;
END;
SET DDD POINT=NNN; OUTPUT; STOP;
%
MACRO DDD A % SPREAD;
MACRO DDD B % SPREAD;
DATA BOTH; MERGE A B; BY TIME;
PROC FREQ DATA=BOTH;
TABLES (PRE_AX PRE_AY PRE_AZ) * (BX BY BZ)/
EXPECTED NOCOL NOROW NOPERCENT CHISQ;
TABLES (PRE_BX PRE_BY PRE_BZ) * (AX AY BZ)/
EXPECTED NOCOL NOROW NOPERCENT CHISQ;
```

VITA

Daniel Scott York was born on 26 November 1955 in Oak Ridge, Tennessee, as the second of three children. He attended Oak Ridge High School where he graduated in 1974.

That same year he entered The University of Tennessee, Knoxville. He showed an interest in animals from the beginning of his studies. During the first year at U.T.K. he concentrated on introductory psychology and biology courses. In one of these courses, he had the chance to read King Solomon's Ring and On Aggression by the Austrian ethologist Konrad Lorenz, and from these readings he became interested in animal behavior.

After having gone to school for eight straight quarters, Mr. York decided to take a break and applied for a six month German work permit. He left for Germany in December 1976, and his planned six months' stay lasted seventeen months. The time in Germany was spent in the small Alpine village of Grainau where Mr. York worked as a waiter in a family-run hotel. As the people he worked with spoke no English, Mr. York was able to develop fluency in German.

On his return to the U.S., Mr. York was privileged to become closely associated with Dr. G. M. Burghardt at U.T.K. It was through his work with Dr. Burghardt that Mr. York's initial fascination with Lorenz and his writings matured into a genuine academic interest in ethology. Mr. York received a Bachelor of Arts degree in August 1979, with a double major in zoology and psychology (academic). At that

time, Mr. York was offered a research position at the Institute for Applied Zoology in Bonn, West Germany, by the German Academic Exchange Service (DAAD). He gladly accepted and once again found himself in Germany.

While at the Institute for Applied Zoology, Mr. York studied interspecific trophallaxis in ants by using P^{32} as a tracer. He also had the opportunity to sit in on advanced lectures in animal ecology and behavior and to visit some of the leading German ethologists and their research facilities. Still, the most important development that occurred in Germany that year for Mr. York was meeting Anna Pia Breuer, of Bonn. They were married in Harrow, borough of London, England, in February 1981, and they enjoyed it so much that they decided to marry once again in Bonn, West Germany, in August 1981!

Mr. York's graduate work at U.T.K. was concentrated on snake behavior. He came to admire this much hated and misunderstood animal group and overcame a general fear of snakes. He received a Master of Science degree with an ethology specialty in the life sciences in December 1983.